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Christian Valentin
Josiane Seghieri Editors

Banded Vegetation Patterning in Arid and Semiarid Environments

Ecological Processes and Consequences for Management

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Banded Vegetation Patterning in Arid and Semiarid Environments

Ecological Processes and Consequences for Management

Foreword by Jean-Claude Menaut and Brian Walker

With 62 Illustrations

Springer

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Cover illustration: Oblique aerial photograph of "typical" tiger bush in Niger, 13°40 N, 2°40 E. (Photo from Christian Valentin.)

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Foreword

Although the pattern of banded landscapes had been recognized in the late 1930s both in East and West Africa, their extent, nature, and ecological importance in arid lands were only realized in the early 1950s. The use of aerial photographs consecrated the names of arcs or stripes in East Africa and of *brousse tigrée*—tiger bush—in West Africa. Curiosity led to attention and study of these most striking and geometric natural landscapes. Most of these studies were isolated, disconnected, and carried out by individuals publishing in different languages. Similar patterns were described in Sahel, East Africa, southern Africa, Australia, and Mexico as formed either of pure grass perennials, of scrubs, or of mixtures of low trees and annual grasses. All possible hypotheses were alleged on the origin and dynamics of such patterns, involving the role of soil heterogeneity (texture or nutrient content), wind erosion, water circulation, and so on.

By the mid-1990s, the body of literature merited some organization and synthesis. The two of us discussed this in the context of understanding ecosystem change at a planning meeting of the Global Change and Terrestrial Ecosystems (GCTE) project of the International Geosphere-Biosphere Program in 1995. Several participants in the GCTE project had an interest in the topic, and they began the task of assembling the team of editors to prepare this book. We are delighted to see it come to fruition.

The content of the book largely relies on a strong body of recent studies conducted in Australia and West Africa, allowing for consistent comparisons and converging conclusions. There was indeed a gratifying degree of convergence of understanding of ecosystem function, given that diverse specialists carried out the research. The work covered a wide variety of disciplines and encompassed the range from theoretical to applied aspects of landscape function: all are represented in this book. The work has not only advanced the understanding of banded landscapes by drawing on existing study techniques, but it has enabled the development of new paradigms of much broader application in landscape design, rehabilitation, and management. However, by lack of adequate studies, some comparable vegetation forms occurring under different soil and geomorphological conditions in East and West Africa have not been taken into consideration and might bring new insights to the question. This book provides new methodological approaches and tracks for further research in the domain.

The book covers the range from methods of study through the science of ecosystem function to the consequences for managing and rehabilitating these widespread semiarid landscapes. It is the first comprehensive account of the subject. We congratulate the editors and chapter authors and are pleased to commend it to students, scientists, and managers interested in the interplay of pattern, process, and function.

Jean-Claude Menaut
Brian Walker

Acknowledgments

The contribution of each author in this book is greatly appreciated. Their efforts to collect a wide array of information, explain the necessary concepts and details, and illustrate the methods with appropriate examples have made this book possible.

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1. Banded Vegetation Patterns and Related Structures

Jean-Marc d'Herbès, Christian Valentin,
David J. Tongway, and Jean-Claude Leprun

Introduction

The study of banded vegetation pattern has proceeded in three steps. The first step consisted of a recognition phase. An early reference to plant formation in western British Somaliland was that of Gillett (1941). Most banded vegetation patterns are difficult to identify on the ground, and their spatial extent was not appreciated until the 1950s when the systematic aerial photographic surveys began (Clos-Arceduc 1956). From the air, the pattern is clearly composed of regularly spaced densely vegetated bands interspersed with bare or less densely vegetated areas. Aerial photographic interpretation proceeded at a number of locations at about the same time, leading to a proliferation of local names for banded vegetation (Boaler and Hodge 1964; White 1969; Mabbutt and Fanning 1987; Montaña, López-Portillo, and Mauchamp 1990). Often these bands or arcs cover broad areas of several square kilometers, forming a distinctive pattern similar to the pelt of a tiger, hence its common name of tiger bush in Africa (Figure 1.1). Similar landscape patterns were called mulga groves in Australia (Slatyer 1961) and mogote in Mexico (Cornet, Delhoume, and Montaña 1988). Many preliminary studies were characterized by "observation/description": the scope of published work was somewhat speculative, exploring a range of explanations for a new and enigmatic landform (Clos-Arceduc 1956; Boaler and Hodge 1964; White 1970).

The second phase involved more experimental studies to test hypotheses suggested in the preliminary phase (Slatyer 1961; Ambouta, 1984; Cornet, Delhoume,

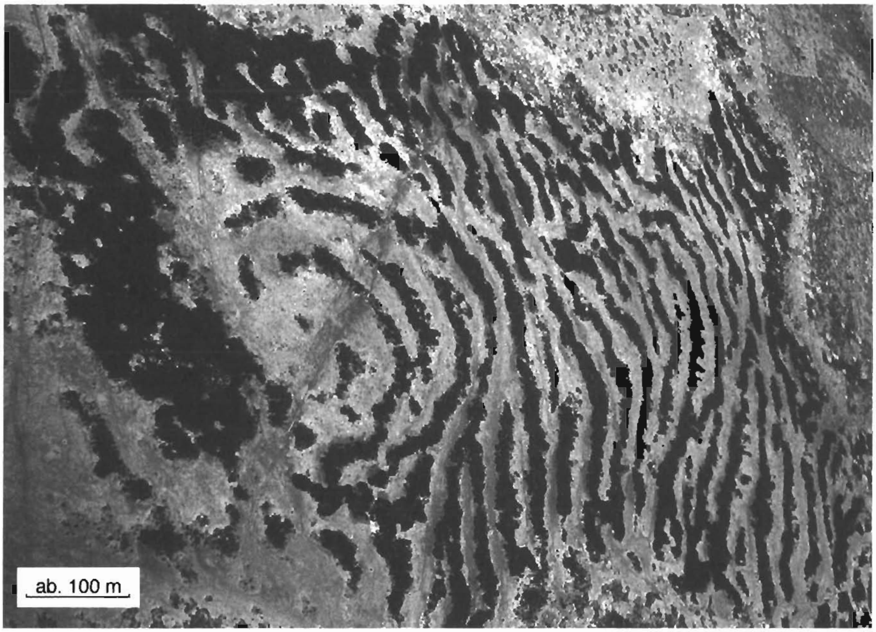

Figure 1.1. Oblique aerial photograph of "typical" tiger bush in Niger, 13°40 N, 2°40 E. (Photo from C. Valentin.)

and Montaña 1988). These included the hydrological functioning (chapters 4 and 5, this volume), ecosystem dynamics (chapters 2, 7 to 9, and 12, this volume), and land management issues (chapters 10 and 11, this volume).

Model building was the most recent phase, and issues such as band initiation and upslope movement were addressed because the field data had been equivocal (chapters 8 and 9, this volume). This step made use of data and hypotheses emerging from the two earlier phases of study to examine the initiation and dynamics of banded landscapes (Mauchamp, Rambal, and Lepart 1994; Thiéry, d'Herbès, and Valentin 1995; Lejeune and Tlidi 1999).

The study of banded landscapes is still somewhat piecemeal. The nature of field work undertaken at different sites reflects the wide variety of available scientific expertise that has been brought to bear on banded landscapes. Progress has therefore been globally uneven. Nevertheless, the state of knowledge now has sufficient maturity to review overall progress and to synthesize the available information.

The aim of this first chapter is to review the main types of banded vegetation patterns at a synoptic scale. As becomes evident, there are many manifestations of vegetation banding, depending on a number of factors. We use a simple classification system based on three simple discriminators:

1. Orientation of the bands with respect to the direction of slope and prevailing wind

2. Degree of contrast between the two phases of the vegetation mosaic
3. Uniformity of the soils beneath the bands and the interbands (Figure 1.2)

Bands Perpendicular to the Slope Direction

Landscapes with Undifferentiated Soils

Landscapes with High Band-Interband Contrast

Tiger Bush. Since the pioneering work of Clos-Arceduc (1956) in Niger, many studies have been devoted to tiger bush both in West Africa (White 1970; Ambouta 1984; Thiéry, d'Herbès, and Valentin 1995; Couteron et al. 2000) and in East Africa (Greenwood 1957; Worral 1960; Wickens and Collier 1971). Typically, five zones were distinguished along transects through tiger bush pattern, extending from the downslope edge of the vegetated band to the core of the next lower vegetated band (Figure 1.3a, b; Thiéry, d'Herbès, and Valentin 1995; Valentin, d'Herbès, and Poesen 1999; chapters 4 and 5, this volume.

The bands aligned with the contour support distinctive communities of annual grasses and forbs, mainly at the upslope margin of the band (Seghieri et al. 1997), with shrubs and trees in the core of the band. The interbands are nearly completely devoid of vegetation. There is little or no difference in soil type between the band and interband (Bromley et al. 1997). Commonly, the bare interband is more steeply

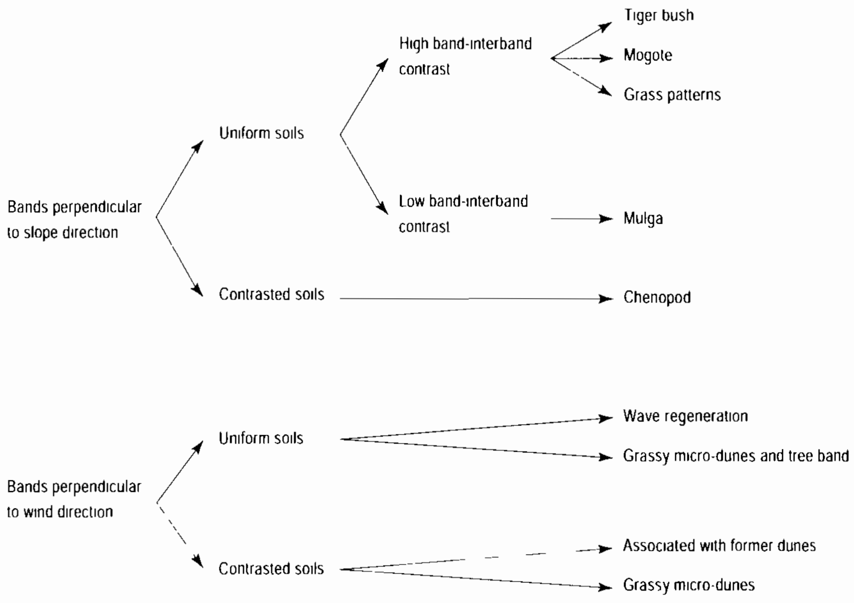

Figure 1.2. Classification of the principal types of banded vegetation pattern.

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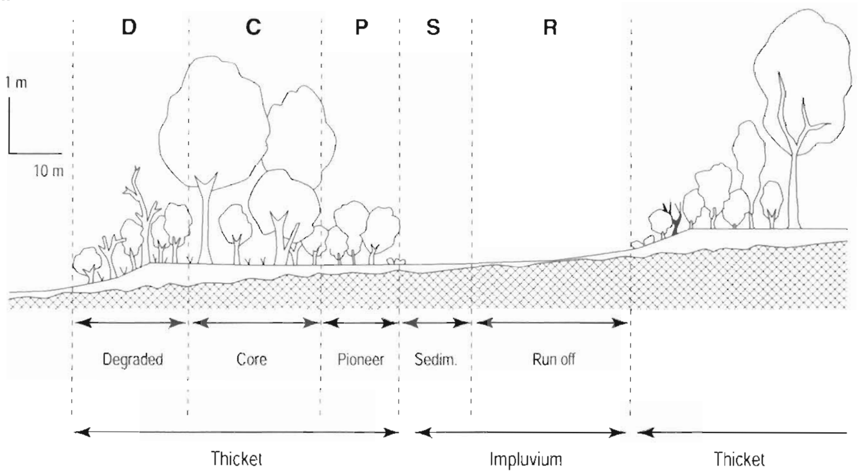

Figure 1.3a. Schematic diagram of a typical transect through the tiger bush in Niger. (Adapted from Thiéry, d'Herbès, and Valentin 1995; Hiernaux and Gérard 1999.)

b

Figure 1.3b. Lateral ground-level view of a degraded downslope edge of tiger bush in Niger. (Photo from C. Valentin.)

sloping than the vegetated band, but there can be local exceptions to this topographic distinction (Chappell et al. 1999). Deposited alluvium at the downslope edge of each interband can result in the formation of a small ridge that acts as a barrier to runoff.

In West Africa, typical tiger bush is found mainly in southwestern Niger, in northern Burkina Faso, and in the adjacent Gourma region in Mali (Figure 1.4). The mean annual rainfall of these regions ranges from 300 to 700 mm yr $^{-1}$ Tiger bush develops on sites with a common array of factors: a semiarid climate, internally draining sites with an underlying sedimentary or metamorphic geology (Leprun 1999).

In Niger, the tiger bush covers 1 million h (chapter 11, this volume) on ferruginous plateaus where the ancient sand deposits have been removed by erosion. When there is a sand cover in Niger or in Mali, banded vegetation does not occur (Figure 1.5; Leprun 1992, 1999; d'Herbès and Valentin 1997).

Variations in band wavelength, band width, and contrast between bands and interbands occur on these plateaus (Figure 1.6, Valentin, d'Herbès and Poesen 1999).

Typically, the wavelength of the bands increases with decreasing slope (d'Herbès, Valentin, and Thiéry 1997; Eddy et al. 1999). Mixtures of band wavelengths can be discerned in close proximity, due to subtle slope differences (Figure 1.7). However, below a critical threshold of slope gradient (0.2% in Niger), the banded

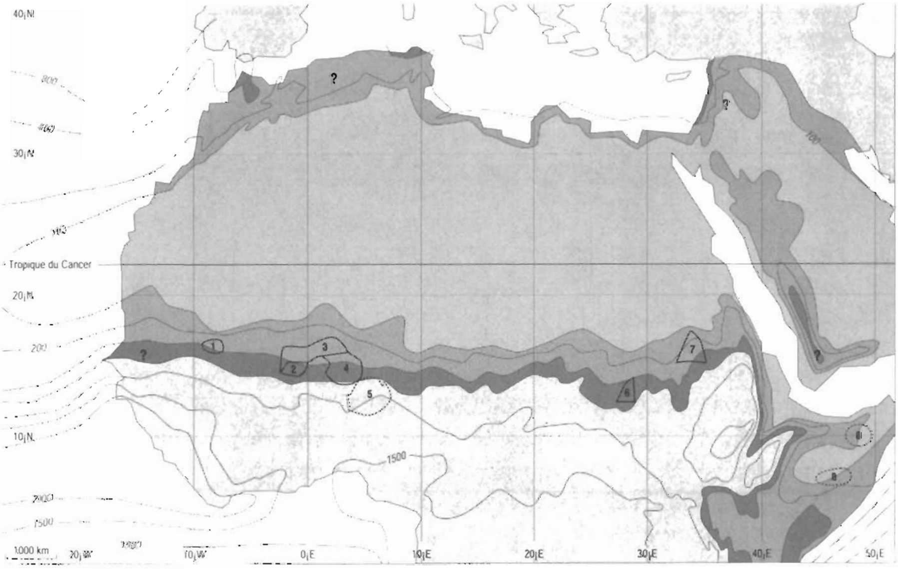

Figure 1.4. Distribution of the tiger bush in northern semiarid zone of Africa according to mean annual precipitation (P). Light gray for P <400 mm ; dark gray for 400 mm < P < 600 mm. Location of banded patterns from (1) Audry and Rossetti 1962; (2, 3, and 4) Leprun 1992, 1999; (5) Zonneveld 1999; (6) Wickens and Collier 1971; (7) Worral 1959; (8) Macfayden 1950. (Adapted from Wickens and Collier 1971; Leprun 1999.)

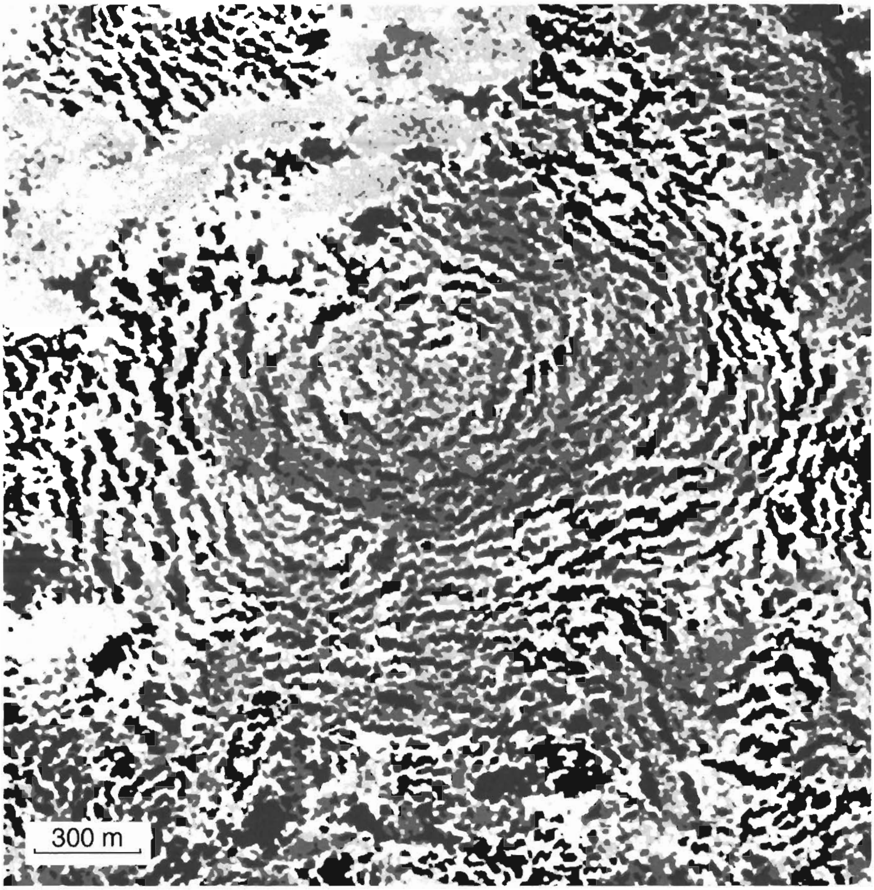

Figure 1.5. Aerial view of tiger bush in Niger on a ferruginous plateau. (Système Probatoire d'Observation de la Terre [SPOT] Panchromatic, 1991.)

pattern disappears and the vegetation assumes a "spotted" distribution (see Figure 1.6). Aguiar and Sala (1999) also report this in Argentina. The slope threshold tends to increase with mean annual rainfall (Valentin, d'Herbès, and Poesen 1999).

The interband/band ratio decreases exponentially with increasing rainfall, varying from 2 under 300 mm of annual rainfall to 0.5 under 700 mm (Valentin and d'Herbès 1999). This relationship was assessed in Niger along a rainfall gradient as well as over a 30 year time sequence (Figure 1.8; Valentin and d'Herbès 1999; Wu, Thurow, and Whisenant 2000). Concurrently, the width of the vegetated bands tends to be reduced with decreasing mean annual rainfall, forming a "dashed" pattern (Ambouta 1984).

Conversely when mean annual rainfall increases, the contrast between the bands and the interbands becomes either less pronounced (fuzzy patterns, Figure 1.9) for slopes gradient of about 0.3% or less banded (dense spotted patterns, Figure 1.9)

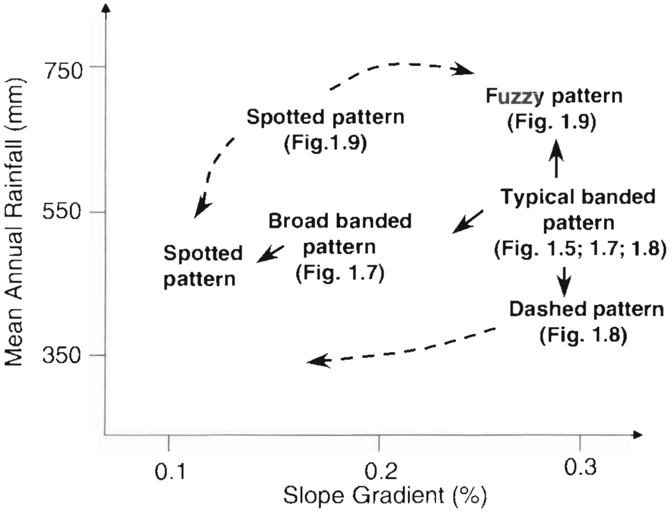

Figure 1.6. Schematic classification of main vegetation patterns in Niger, according to mean annual rainfall and slope. Dark arrows indicate potential transition between pattern types; dashed arrows represent potential spatial extension of the pattern. (Adapted from Valentin, d'Herbès, and Poesen 1999.)

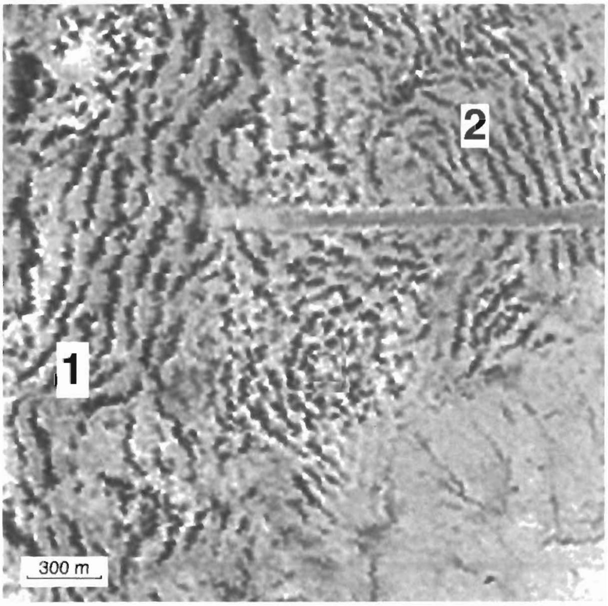

Figure 1.7. Co-occurrence of "broad banded" (zone 1: slope < 0.20%) and "typical" (zone 2: slope 0.25%) vegetation patterns on the same plateau in Niger (mean annual rainfall, 60 mm). (SPOT Panchromatic 1991.)

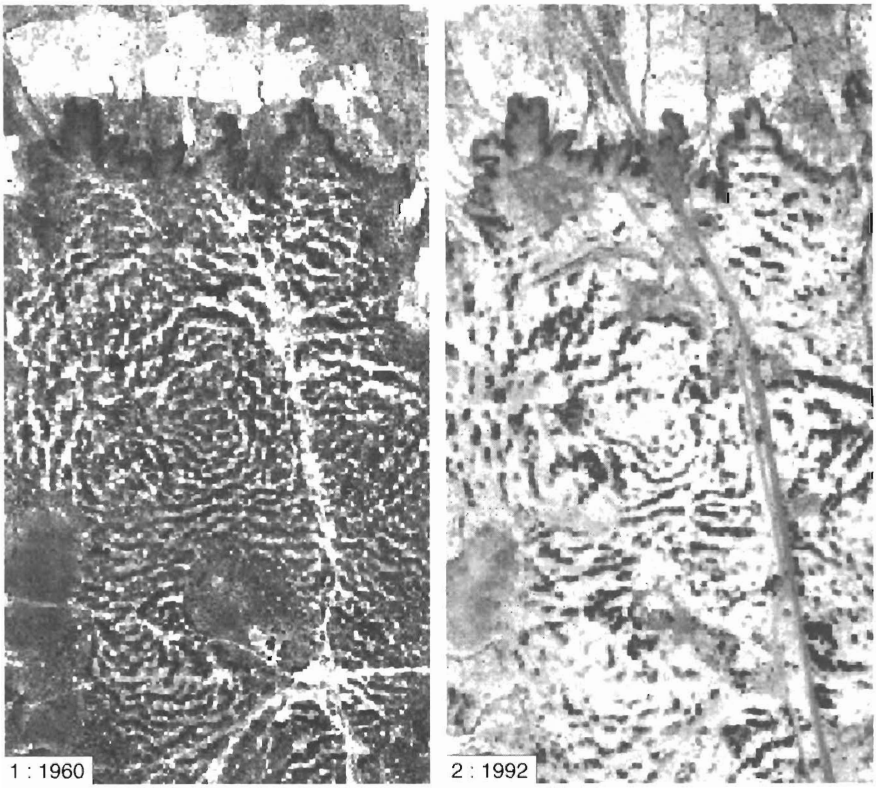

Figure 1.8. Degradation of a "typical" tiger bush pattern (1, 1960) to a "dashed" pattern (2, 1992) due to greatly increased anthropic pressure in terms if firewood collection and a decrease in mean annual rainfall. (From Wu, Thurow, and Whisenant, 2000. Permission courtesy of Blackwell Science Ltd.)

The Mogote. Mogote is the local name for the banded vegetation pattern studied in the Chihuahuan Desert of northern Mexico (Cornet, Delhoume, and Montaña 1988; Montaña, López-Portillo, and Mauchamp 1990; Cornet et al. 1992; Montaña 1992; Mauchamp, Rambal, and Lepart 1994; Delhoume 1995; López-Portillo and Montaña 1999). This pattern is very similar to tiger bush (Figure 1.10) but develops under more arid conditions than in West Africa.

The region is located at about 1100 m above sea level, receives a mean annual rainfall of only 283 mm (variation coefficient of 23%; Mauchamp and Janeau 1993). These banded patterns occur in the lower part of the hillslopes on slope gradients of about 0.5%. The substrates include alluvia and colluvia. The soil texture varies from clay to sandy-clay loam with similar surface crusts to those observed in tiger bush (Figure 1.11; Janeau, Mauchamp, and Tarin 1999). There is no difference in soil type between the bands and the interbands except for gilgai microrelief in the upper layers of the vegetated bands (Delhoume 1995). The trees of the

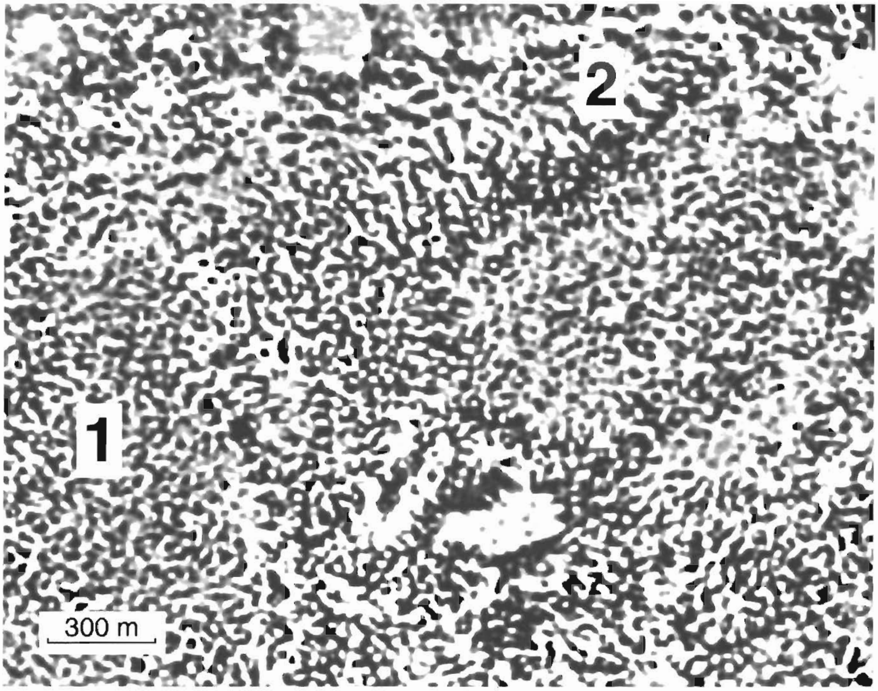

Figure 1.9. Co-occurrence of "spotted" (zone 1, slope = 0.20%) and "fuzzy" (zone 2, slope = 0.35%) patterns on the same plateau (680 mm annual rainfall) in Niger. (SPOT Panchromatic 1991.)

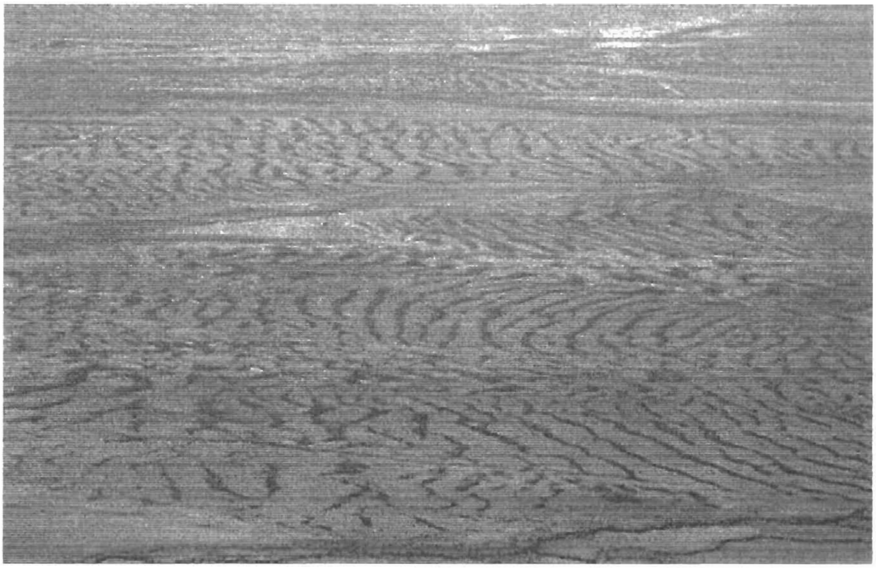

Figure 1.10. Oblique aerial view of the "mogote" pattern in northern Mexico. (Photo from J.P. Delhoume.)

Figure 1.11. Ground-level lateral view of the upslope fringe of the vegetation band in the mogote banded vegetation pattern in northern Mexico. (Photo from C. Valentin.)

mogote are shorter than in West Africa (2.5 m compared with 7 m) and the grass is perennial rather than annual (chapter 5, this volume). The interband/band ratio (3 to 4) is much higher than in Niger.

Grass Patterns. Vegetation patterns consisting of alternating bands of grass and almost bare soil oriented on the contour in the Sudan and Somalia (Macfayden 1950; Worrall 1959; Boaler and Hodge 1964; Hemming 1965) were among the earliest recognized banded landscapes. There are no differences in soil type reported for the grassy and the bare bands, a similar situation to tiger bush and the mogote. These banded landscapes are located on very gentle slopes of about 0.5% under arid and semiarid conditions (100 to 400 mm rainfall yr^{-1}). Soil textures range from loam to sand. The interband/band ratio of 2 is similar to that of the drier tiger bush regions in West Africa.

Landscapes with Low Band-Interband Contrast

Mulga. There are extensive banded landscapes in Australia where the tree component is dominated by mulga (*Acacia aneura*), with canopy covers between 20 and 40% (Figure 1.12). These lands have characteristics typical of banded landscapes everywhere: low slopes (0.2 to 2%), sheet-flow of runoff water and annual rainfall between 200 and 500 mm. Rainfall seasonality varies between uniform to summer dominance. Landforms range from slightly convex through planar to slightly concave. Some landscapes are located on tertiary residual plateaus, similar to those in Niger, whereas others are on piedmont slopes and alluvial plains

Figure 1.12. Oblique aerial view of groved mulga in Australia. (Photo from G. Griffin.)

(Mabbutt and Fanning 1987). The soil textures vary from clayey-sand to sandy-clay and are generally acid, with a slight increase in texture with depth. Parent materials are sandstones. Physical crusting of the surface soil is ubiquitous. Typically, banding is narrower on finer-textured soils. At the higher rainfall end, the bands, or groves, the common name in Australia, have a dense perennial grassland on the upslope edge of the band (Figure 1.13a, b). At lower rainfalls, there may be a sparse (<4% cover), unpatterned perennial grass or shrub understory. Intergrove zones are typically bare (Figure 1.13b) but may grow ephemeral herbage after rain. There are large areas in Western Australia where the banding is underlain by a silica-cemented hardpan (Bettenay and Churchward 1974) varying from 15 to 100 cm below the surface.

Banded Pattern with Differentiated Soil Types

Chenopod Shrublands

Extensive areas of banded chenopod shrublands occur in eastern Australia, associated with the Barrier Range (Figure 1.14). These occur on typical landforms and climate for banded vegetation: gentle planar slopes associated with outwash plains from the ranges, which are a maximum of 300 m above the surrounding plain, 200 to 250 mm annual rainfall. The slopes extend to the east and west of the range, which is oriented north–south. These banded landscapes are unusual in having distinctively different texture profiles associated with the vegetated band and the bare interband. The former zone is characterized by deep cracking self-mulching calcareous clays with gilgai microrelief, whereas the interband zone is composed of

a

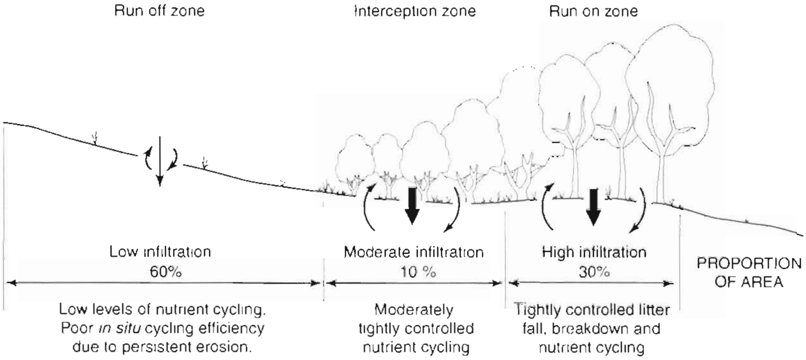

Figure 1.13a. Schematic diagram of a typical transect through groved mulga in Australia. (Adapted from Noble, Greene, and Müller 1998; Tongway and Ludwig 1990.)

b

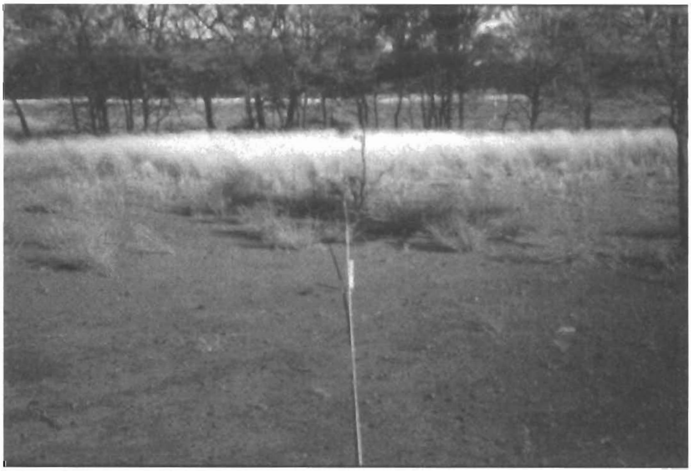

Figure 1.13b. Lateral ground-level view of groved mulga in Australia. (Photo from D.J. Tongway.)

a texture-contrast soil with a noncalcareous loamy A horizon about 10 cm deep, overlying a red well-structured clay (Wilson, Tupper, and Tongway 1982). The interband is frequently covered by stone and is bare of vegetation. There is a large differential in infiltration rate between these soils, and runoff water feeds the vegetated band from as little as 4 mm of rain (Dunkerley and Brown 1995). Typically, chenopod shrubs, *Atriplex* and *Maireana* species, occupy the band, but when infrequent summer rains occur, dense stands of the perennial grass *Astrebla* germinate and persist as long as the soil water supply remains. The clay materials were deposited by aeolian action about 16,000 years B.P. and have their origin in ancient lake basins to the west (Chartres 1982).

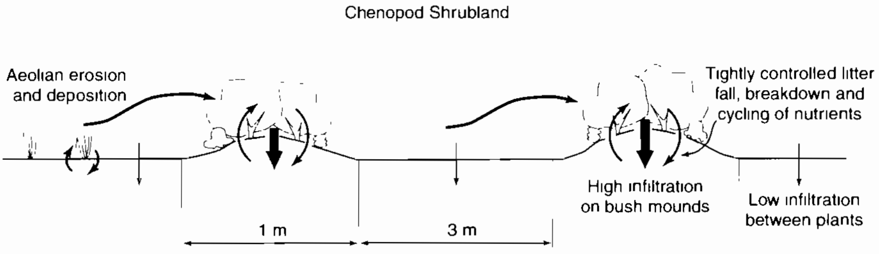

Figure 1.14. Schematic diagram of a typical transect through chenopod. (Adapted from Tongway 1993.)

Bands Perpendicular to the Wind Direction

Landscapes with Undifferentiated Soils

Wave Regeneration

Wave-regenerating forests consist of stripes of trees perpendicular to the prevailing wind direction, with older and dying trees in the windward edge and a seedling regrowth on the lee side of each band. These patterns have been recognized in northeastern United States (Sprugel 1976; Sprugel and Bormann 1981), central Japan (Kohyama 1988; Sato and Iwasa 1993), and eastern Tierra del Fuego (Puigdefábregas et al. 1999).

Using a model based on a cellular-automata simulation, Sato and Iwasa (1993) assumed that trees die if they are taller, by a critical threshold value, than their windward neighbors (Figure 1.15). The major cause of death was the desiccation of canopies in winter. A similar model (Puigdefábregas et al. 1999) also generated bands from initially random patterns. The authors hypothesized that tree clusters produce cone-shaped wind shadows that protect larger clusters on their leeward side, this process being repeated and enlarged through a positive feedback mechanism. The model showed that the higher the tree growth, the longer the wavelengths and the higher the wave propagation rates. More lethal winds led to shorter wavelengths and lower propagation rates.

Alternating Microdunes and Bands

More complex banded patterns have been reported in Mauritania by Audry and Rossetti (1962), in Mali by Leprun (1992, 1999), and in Australia by Mabbutt and Fanning (1987). These consist of a band system oriented nearly perpendicular to the wind direction comprising a sandy grass-covered microdune (Figure 1.16), a bare sloping crusted band, and a dense vegetated band including some trees or shrubs. These patterns have been attributed to alternate wind action and sheet water flow, perhaps representing climatic variations over decade to century time scales.

Figure 1.15. Schematic diagram of a typical transect in a wave regenerating forest. (From Sprugel 1976.)

Bands with Soil-Type Differentiation

Bands Associated with Former Dunes

In semiarid regions, to account for banded patterns that maintained their spatial orientation irrespective of topographic variation, they have been associated with leveled former dune fields (Figure 1.17). These have been described mainly in northern Nigeria (Clayton 1966, 1969; Zonneveld 1999) and in the Kimberley district of northwest Australia (Goudie, Sands, and Livingston 1992).

Grassy Microdunes

Desert ripples in the Salt Lake Desert (United States) are small transverse dunes, 9 to 150 m long, 25 to 90 cm high, with a crest interval of 3 to 15 m. They are par-

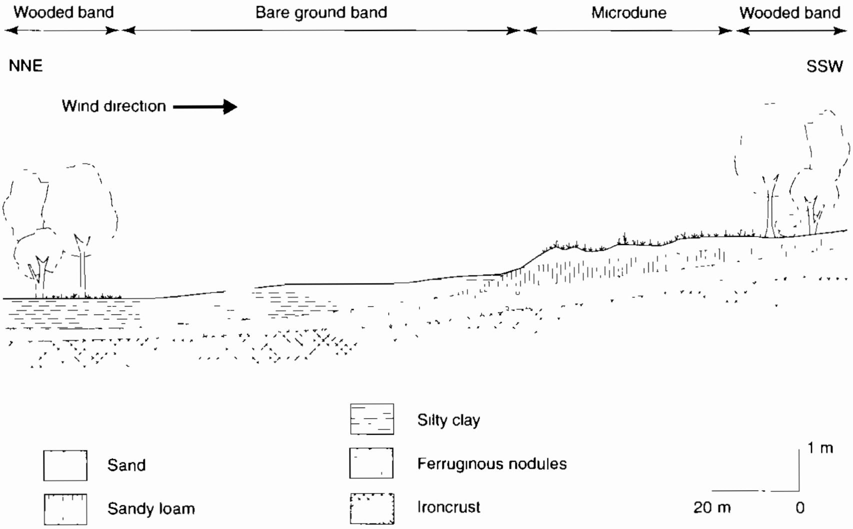

Figure 1.16. Schematic diagram of a typical transect alternating microdunes and bands in Mali (Adapted from Leprun 1999.)

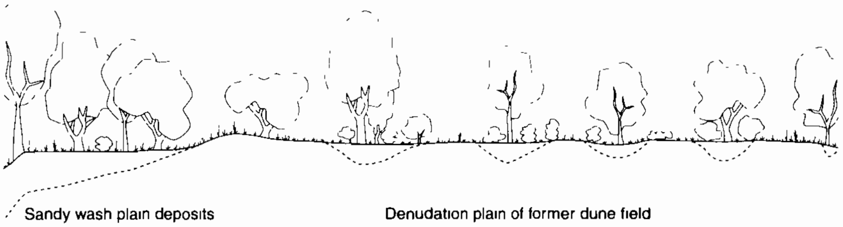

Figure 1.17. Schematic diagram of a transect in banded vegetation associated with former dunes in Nigeria. (Adapted from Zonneveld 1999.)

tially stabilized by vegetation cover on the ripple crests and by caliche plating of the trough floors (Figure 1.18). Ives (1946) invoked conventional aerodynamic theory to account for the aeolian origin of these features, where sand accumulated around obstacles in a characteristic ripple pattern. Similarly, White (1969, 1971) suggested that the accumulation of aeolian sand trapped material by isolated plants as shadow dunes might act as a nucleus of the development of grassy microdunes over saline and alkaline alluvial soils in Jordan. He also observed similar patterns in the Iraq-Syrian border areas.

Other Banded Patterns

Mediterranean terracettes (Figure 1.19) develop on steeper slopes (10 to 60%) and at finer scales but are strongly analogous with the high-contrasted banded vegetation patterns on uniform soils (see Figure 1.2). They have been described in southeastern Spain under mean annual rainfall ranging from 300 to 400 mm (Puigdefábregas and Sanchez 1996; Bergkamp, Cerdà, and Imeson 1999).

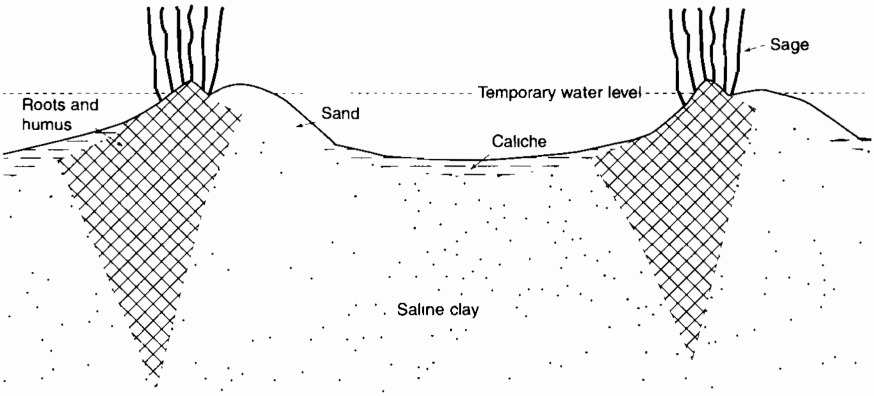

Figure 1.18. Schematic diagram of desert ripple morphology associated with small transverse dunes on caliche. (After Ives 1946. Reprinted by permission of the *American Journal of Science.*)

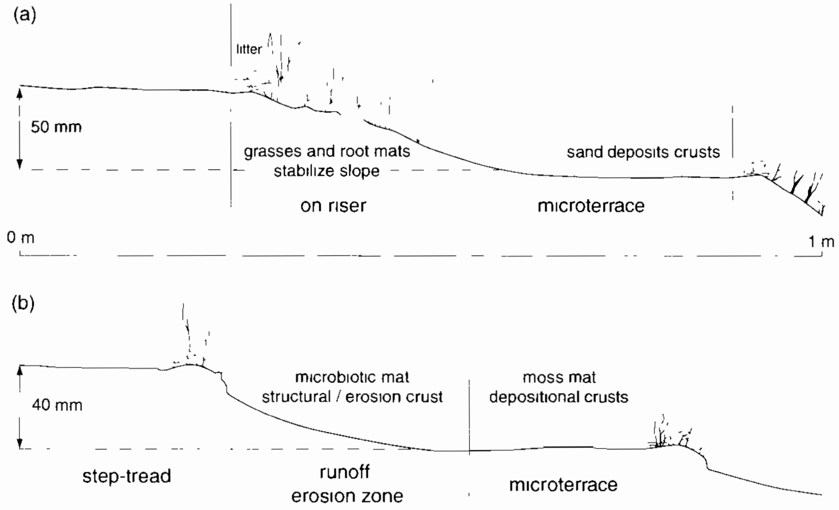

Figure 1.19. Schematic diagram of litter dams structures (a) with vegetation located on the slope and (b) with vegetation located at the edge of the terrace. (Reprinted from Catena 37(1/2), Eddy et al., Vegetation arcs and litter dams: Similarities and differences, pp. 57–73, Copyright 1999, with permission from Elsevier Science.)

Even smaller-scaled vegetation bands patterns have been reported from a number of locations, such as those associated with litter dams (Eddy et al. 1999) and sediment deposition (Bryan and Brun 1999). In both cases, slope profiles and crust distribution along the transect lines are similar to those observed in the tiger bush, suggesting similar controlling processes (Figure 1.20). It is possible that these structures are meta-stable transitional states on a degradation gradient.

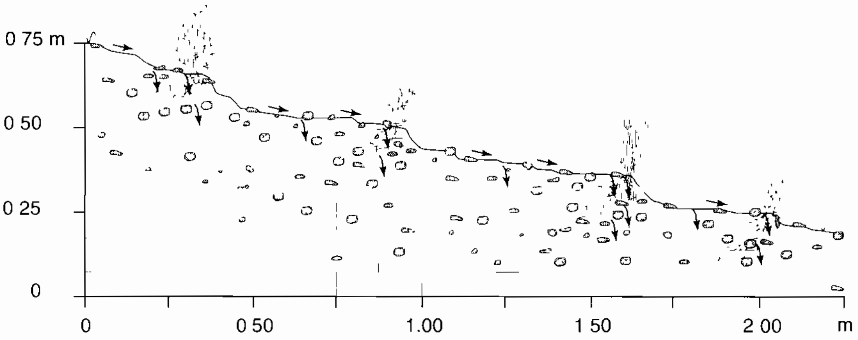

Figure 1.20 Schematic diagram of a microterrace structure in southern Spain. (Reprinted from Catena 37, Bergkamp, Cerdà, and Imeson, Magnitude-frequency analysis of water redistribution along a climate gradient in Spain, pp 129–146, Copyright 1999, with permission from Elsevier Science.)

Summary

This chapter has described the range and global distribution of banded vegetation landscapes that have been reported in the literature to date. There are similar landscape patterns on different continents (e.g., the tiger bush and the mogote) and different pattern types in neighboring regions (e.g., the groved mulga and the patterned chenopod shrubland). The variety of expressions of the banded landscape phenomenon probably accounts for apparently conflicting theories about the origin and functioning of these strikingly geometric landscapes. The following chapters of this volume provide a synthesis of what is currently known, linking the scientific information with management imperatives.

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2. Theories on the Origins, Maintenance, Dynamics, and Functioning of Banded Landscapes

David J. Tongway and John A. Ludwig

Introduction

In this chapter, we explore the whys and hows of banded landscapes: (1) why do they form? (2) how are they maintained? (3) how do they move? (4) how do they work to conserve resources? In addition, we discuss how understanding these processes contributes to advancing heterogeneity theory in landscape ecology generally. Where banded landscapes occur and what forms they take were described in chapter 1. Such landscapes occur in Africa, Australia, and the Americas, and perhaps elsewhere, and are often called two-phase mosaics because they form bands of bare soil alternating with bands of perennial vegetation. They tend to be situated on low planar slopes and are characterized by the long axis of the bands being oriented along the contours of these slopes.

The advent of aerial photography revealed the regularity of these strikingly repeating patterns, which might otherwise have gone undocumented for a long time (Greenwood 1957). Ground surveys commenced after World War II, seeking to define national land and water resources in Africa (Macfayden 1950a) and Australia (Perry 1960; Mabbutt et al. 1963). These surveyors used aerial photographs to map the extent of banded landscapes. A number of researchers speculated on the origins, modus operandi, and dynamics of these landscapes (Macfayden 1950b; Clos-Arceduc 1956; Greenwood 1957; Litchfield and Mabbutt 1962; Mabbutt 1963; Worral 1959; Ruxton & Berry 1960; Slatyer 1961; Boaler and Hodge 1964). In this chapter, we briefly reexamine these speculations and hypotheses in the light of our current knowledge about banded landscapes, leaving details to those authors contributing to chapters 4 to 9 in this book. We also describe a theoretical framework on how banded landscapes function to conserve limited resources.

Why Banded Landscapes?

There are basically two types of banded landscape. The first, and most common type, occurs on medium-textured soils (sandy-loam to clay-loam) with little or no soil profile texture differences between the bare and vegetated zones. This type occurs in Somaliland (Macfayden 1950a), Niger Republic (White 1970; Ambouta 1984), Nigeria (Clayton 1957; Grove 1957, 1958), Mexico (Cornet, Delhoume, and Montaña 1987), and Australia (Slatyer 1961; Litchfield and Mabbutt 1962; Mabbutt and Fanning 1987). This banding is characterized by strips of shrub or tree thickets separated by substantially bare ground. Bare zones always had noticeable physical crusts that were deemed to have low infiltration rates and so initiated runoff soon after the commencement of rainfall.

The second banding type has a marked difference in soil texture between the vegetated and bare zone. Smectitic clays, with swell shrink properties and characteristic gilgai formations, are associated with the vegetation, whereas massive loams or texture-contrast and stony-surfaced soils form the bare zones. This type occurs in the Sudan (Worral 1959) and Australia (Chartres 1982; Upton 1983; Goudie, Sands, and Livingstone 1992; Dunkerley and Brown 1995; Macdonald, Melville, and White 1999). Typically, this type has grassland or chenopod shrubland forming the vegetation bands; bare zones are often crusted or stony.

There were, and still are, many different speculative starting points for why banded landscapes form. Some suggest that banding is recent, forming only in historical times from a uniform cover of vegetation due to the impacts of land use by humans (Hemming 1965; Wickens and Collier 1971). Others suggest that banding formed over Holocene time due to climatic shifts (Clos-Arceduc 1956; Boaler and Hodge 1964) or through geomorphic processes that shaped landscapes into their current form (Litchfield and Mabbutt 1962; Cornet, Delhoume, and Montaña 1988). Biotic causes were also suggested such as the slumping of termite mounds to form a resistance to overland flow (Macfayden 1950a). As no one has actually observed banded landscapes forming ab initio, this area remains speculative (chapter 8, this volume).

The relative roles of wind and water as agents forming banding patterns probably shifts as both climatic conditions and land-use changes occur, such as seen with accelerated desertification during droughts (Rossetti 1996). The susceptibility of the soil to either type of erosion will also be a consideration. However, under normal conditions, water is now seen as the primary causal agent, with wind a minor factor (chapters 8 and 9, this volume). Ives (1946) reported vegetation arcs in the western deserts of the United States, but these involved a linear dune system, which is outside the scope of this book. Several authors have noted that water that flows as a thin sheet over a gentle landform is an invariable characteristic of banded landscapes. Greene, Valentin, and Esteves (chapter 4) and Galle, Brouwer, and Delhoume (chapter 5) of this volume cover this in detail. Although banded landscapes can vary from having gentle slopes (e.g., 1:700) to relatively steep slopes (e.g., 1:50), if the soil type and surface condition promotes runoff as sheet-flow, banded patterns often form. Banded vegetation is not found on landscapes with incised water drainage channels, and indeed banding patterns were noted to disappear when incised channels appeared on the landscape (Macfayden 1950b; Hemming 1965). Recent simulation models predict that bands in vegetation may appear spontaneously on landforms with gentle slopes where rainwater flows over the surface in mildly turbulent waves with some lateral transfers (Dunkerley 1997; chapter 9, this volume).

In summary, we conclude that banded vegetation forms on landscapes where there is a high probability that slopes and soil surface crusts promote the frequent occurrence of runoff in the form of thin overland sheet-flow. Even small obstructions to this flow can trigger positive feedback mechanisms to cause sediment deposition and water infiltration and, hence, vegetation development in the shape of a wave, arc, or band. We submit this as the central theorem of band formation, although other theories based on vegetation change response to a variety of climate and/or land-use and/or fire regimes changes may apply from place to place.

How Are Banded Landscapes Maintained?

The apparent stability and longevity of banded landscapes raises the issue of how these structures are maintained over time. Several inferences about the maintenance of bands have been made from the early observations, and these have been the subject of detailed field work in more recent times (chapters 4, 5, 7, and 8, this volume). The following processes are hypothesized as being key to the maintenance of banded landscapes:

1. *Obstruction to overland flow*—When the velocity of runoff as sheet-flow slows due to an obstruction (e.g., a vegetation band), the transporting capacity of the flow is correspondingly much lower (Moss 1979). In fact, sediment carrying capacity varies as the fifth power of the flow rate (Hemming 1965). Thus, a small decrease in flow rate greatly increases the rate of sedimentation. Also, organic matter is transported by this flow and is deposited in or just above the vegetation band where the water flow is slowed (Macfayden 1950a,b). Further, infiltration is greater because there is more time for water to recharge soil water stores. Thus, these obstruction-sedimentation-infiltration processes are positive feedback mechanisms that maintain vegetation bands.
2. *Differential infiltration*—Soils in the bare and vegetated bands have inherently different infiltration rates, being low in the bare zone and high in the vegetated zone (Wickens and Collier 1971; Greene 1992; Galle, Ehrmann, and Peugeot 1999; chapter 5, this volume). This effect is in addition to the slowed flow rate effect noted above. For example, Goodspeed and Winkworth (1978) reported

that mulga bands absorbed about 250 mm of water after a 210-mm rainfall, whereas bare interbands absorbed only 43 mm from the same rainfall (i.e., 80% of the water was shed as runoff) (Greene 1992). This phenomenon is so obvious in the field that bare slopes are often called runoff areas or source zones (i.e., the source of water and sediments) and vegetation bands are runon areas or sink zones (Greenwood 1957; White 1970).

Although Wickens and Collier (1971) stated that a loose sandy surface is necessary for high infiltration within a vegetation band and for the mulching action that occurs during the soil-drying phase, subsequent studies have not supported this (Hodge, quoted in Greenwood 1957; Mabbutt and Fanning 1987; Tongway and Ludwig 1990). In fact, Greene (1992) has demonstrated that it is the abundance of macropores (formed by the process of bioturbation) within soils of the bands that account for their high infiltration rates (chapter 4, this volume). Deeper leaching of soluble salts in vegetation bands compared with bare zones also provides evidence of deeper infiltration (Boaler and Hodge 1962; Macdonald, Melville, and White 1999; White 1969).

Greenwood (1957) and Wickens and Collier (1971) identify bare zones as having low infiltration due to crusts formed by the percussive action of raindrops. This property was recognized as having some significance in the relative proportions of the bare and banded zones (Valentin and d'Herbès 1999). The respective widths are indicative of the area needed for water harvesting from the bare zone to supply the water required to support the phytomass in the vegetated zone; that is, there is a degree of self-organization in banded landscapes (Seghieri and Galle 1999; Valentin, d'Herbès, and Poeson 1999). This synthesis implies that the bare runoff zone and the vegetated runon zone comprise a "basic functional unit," somewhat independent of larger-scale landscape processes. Many later studies acknowledged this proposition by sampling landscapes in a "paired runoff-runon" sequence (Cornet, Delhoume, and Montaña 1988; Ludwig and Tongway 1995; Mauchamp, Rambal, and Lepart 1994; Montaña, López-Portillo, and Mauchamp 1990; Montaña 1992; Thiéry, d'Hèrbès, and Valetin 1995; chapter 9, this volume).

3. *Efficient nutrient cycling*—Although water-driven processes are considered to be the primary forces in forming and maintaining banded landscapes, there are other processes such as nutrient cycling that augment these water processes (Tongway 1990). Organic matter (e.g., litter, seeds, and animal dung) are transported from bare zones and deposited in vegetation bands (Macfayden 1950a; Greenwood 1957; Hemming 1965). Few authors took this matter any further in terms of the process of nutrient cycling and its role in maintenance of banded landscapes. Tongway and Ludwig (1990) reported that the soil in mulga bands contained up to three times the nutrient concentration to that of upslope runoff zones. This differential was attributed to effective capture of organic matter carried by sheet-flow by the bands and subsequently highly efficient nutrient cycling involving in situ decomposition of litter and dung within these bands. Recent work by Guillaume and associates (1999) confirmed this proposition in Niger.

4. *Torrential rainfall*—The range of annual average rainfall is wide in regions with banded landscapes. Regions with higher average rainfall such as parts of Nigeria and Somalia are always markedly seasonal (summer monsoons) (Boaler and Hodge 1964; Clayton 1966). Regions with lower annual rainfall averages, such as in Jordan (50 mm) and in eastern Australia rangelands (250 to 400 mm), tend to have aseasonal patterns (evenly distributed throughout the year) (Clewett et al. 1994; White 1969), with most rains falling as low-intensity showers. Mexico had both a low annual average and summer seasonal rain (Montaña, López-Portillo, and Mauchamp 1990).

The quantity of annual average rainfall is therefore not a critical factor, within limits, in the maintenance of banded landscapes. Overall soil water availability to biota must be limited either by tight seasonal supply or by chronic shortage (i.e., a large deficit between precipitation and evaporation). In seasonal rainfall regions, soil water stored from summer rains in the soil profile beneath tree thickets or bands can then be exploited during the dry season; this fosters the survival of the deep-rooted trees and shrubs in the band. Rainfall rate is significant insofar as runoff from the bare zone into the vegetated zone must occur, and that the runoff should be in the form of sheet-flow. Galle, Brouwer, and Delhoume (chapter 5, this volume) discuss this aspect in detail, citing a number of field examples. Banded landscapes have been observed to disappear over a period of 30 years and are replaced with nonpatterned country when the water-shedding nature of interbands cease due to a thin sheet of aeolian sand in northeastern Mauritania (Rossetti 1996). This must be regarded as an example of desertification. The proposition that rainfall must be torrential (Wickens and Collier 1971) cannot be sustained as a generality because banded landscapes occur in aseasonal rainfall regions (e.g., Jordan and Australia), where rainfall rates rarely exceed 30 mm h^{-1}. However, runoff occurs in about 3 minutes at this intensity (Tongway and Ludwig 1990).

In summary, the theory that seems to best explain the maintenance of banded landscapes is that vegetation bands form obstructions that slow sheet-flow, resulting in the deposition of sediment and minor organic matter such as animal dung within the bands. These materials, along with higher water stores from greater infiltration and litter from the vegetation in the band, are positive feedbacks that build and maintain the bands.

Do Vegetation Bands Move Upslope?

The upslope movement of vegetation bands has been a central issue from the earliest observations (Worral 1959; Ruxton and Berry 1960), and remains a matter of contention when comparing the behavior of different landscapes. These authors have observed upslope movements of about 1 m yr^{-1} in gilgaied patterns in the Sudan, hypothesizing that new soil cracks and sink holes forming on the upslope edge of the vegetation band are responsible for the movement upslope. Leprun (1992, 1999) provided hard evidence of movement in the range of 0.2 to 0.7 m yr^{-1} over a period of 21 years in Mali. We have not specifically studied the movement of mulga bands in eastern Australia, but the presence of young trees and shrubs on the upslope edge of bands, and old and dead trees on the downslope edge, suggest that the bands do move. These movements may be highly episodic, at long time intervals, perhaps responding to cyclical climatic variation, rather than continuous under the current climatic regime (Ludwig and Tongway 1995; Anderson and Hodgkinson 1997; Tongway and Ludwig 1990). However, Mabbutt and Fanning (1987) refute the likelihood of upslope movement of mulga bands in Western Australia based on their observations of the age structure of trees across the bands and the shape of an edaphic duripan that exists at shallow depths under the Western Australian banded mulga.

Recent studies of the landscape processes responsible for upslope band movement in Mexico and Africa have come from examination of the patterns of germination on the upslope and downslope edges of the dense vegetation bands (Montaña, López-Portillo, and Mauchamp 1990; Seghieri, Floret, and Ponanier 1994: Seghieri et al. 1997; chapter 7, this volume). Germination is invariably highly skewed, with most seedlings being found on the upslope edge. This is prima facie evidence but not sufficient in itself to prove the hypothesis. Similarly, perennial grasses are most abundant on the upslope edge of mulga bands in eastern Australia (Tongway and Ludwig 1990). This was attributed to the relatively high frequency of small runoff events that moistened soils to only a shallow depth at the upslope edge of mulga bands, favoring grasses; trees and shrubs being favored by deeper infiltration at longer intervals (Anderson and Hodgkinson 1997). Large rainfall events, in which runoff is sufficient to saturate the mulga band, have a relatively low frequency in this region of eastern Australia (Clewett et al. 1994). The downslope edge of the bands has no grass at any time and is characterized by having an erosion terrace approximately 10 cm high, indicating that erosion is at least a periodic process.

Insights into the mechanism of upslope movement of vegetation bands were demonstrated by Montaña (1992) and Montaña and associates (chapter 7, this volume) when a study over a period of 8 years revealed the upslope movement of a peak of species richness. Another study comparing vegetation germination patterns in Niger and Burkina Faso (Couteron et al. 1996) demonstrated that vegetation bands in Niger appear to migrate upslope while there was no movement in Burkina Faso. This is attributed to differences in soil texture, and hence soil water dynamics. A more detailed examination of these fine-scale issues is found in chapter 8 of this volume. The observations reported above are also consistent with an "expansion-contraction" model. Plant establishment advances on the upslope edge of the thicket when seasonal conditions and anthropic stress levels permit but retreats when conditions are more adverse. In some banded landscapes, this is a seasonal cyclicity.

In summary, it seems most likely that movement of vegetation bands is the consequence of subtle differences in the availability of water over time at the immediate upslope edge of the band. This may be due to terrain shape (Thiéry, d'Hèrbes, and Valentin 1995), where a decrease in slope slows water flow, hence increasing infiltration at the upslope edge of vegetation bands, or due to the vegetation structure itself, acting as an obstruction to flow as discussed earlier, or both. In either case, movement is probably a two-stage process (Ambouta 1984): (1) the contraction of the downslope edge during dry years due to plant death, thus narrowing the band, and (2) upslope germination of pioneer plants in the upslope edge in seasons of good rainfall, thus widening the band.

How Do Banded Landscapes Work to Conserve Resources?

Early observations of vegetation banding took a broad or "whole system" view of how these landscapes form by erosion processes (Macfayden 1950a; Hemming 1965; White 1970, 1971; Mabbutt and Fanning 1987), probably because these expert observers were primarily interested in regional geomorphology. More recent studies on banding have tended to use only small portions of the landscape to address specific detailed questions, such as band movement (Montaña 1992; Seghieri et al. 1997; Dunkerley and Brown 1995; Couteron et al. 2000). Recently, Australian work has again taken up the "whole landscape" questions but now focused on theoretical predictions about how these and other landscapes function as resource-conserving systems, based on field data integrating terrain, soil, and vegetation patterns (Ludwig and Tongway 1995, 1997; Tongway and Ludwig 1997a).

A framework has been developed to formalize how semiarid landscapes function to regulate, conserve, use, and cycle limited resources, both spatially and temporally (Figure 2.1). This trigger-transfer-reserve-pulse framework depicts with arrows and elements how a pulse of activity can be triggered by a rainfall input at a given point in time. Rainwater is redistributed or transferred spatially (i.e., runoff) and captured by structures within the landscape (i.e., bands, patches, thickets) that store this runoff as a resource reserve, along with the sediments and litter it carries. If the quantity of these water and nutrient resources exceeds required thresholds, then a pulse of activity (e.g., plant growth) occurs. This pulse will normally feed back materials (e.g., ploughback seeds and recycle nutrients) and structures (e.g., increase the number of plant stem obstructions) to the system. However, some plant growth can be consumed by animals (livestock) as forage and be lost from the system or be consumed as fuel by fire.

The abundance of obstructions (vegetation patches and bands) and their relative permanence within the landscape is critical to how well the system functions to capture, store, and recycle resources (water and nutrients) within the system. How well landscapes function to conserve limited resources is vital for these semiarid systems (chapters 4 and 5, this volume).

Our landscape function approach and framework is based on theoretical predictions by Noy-Meir (1973, 1979, 1981), which indicated that when overall water supply was limiting, more biomass would be produced per unit area, if rainwater is concentrated into runon sinks (bands, patches) rather than being uniformly spread over the landscape. This invoked the concept of a threshold amount of soil water needed to produce a pulse of biological activity. If upslope runoff water from

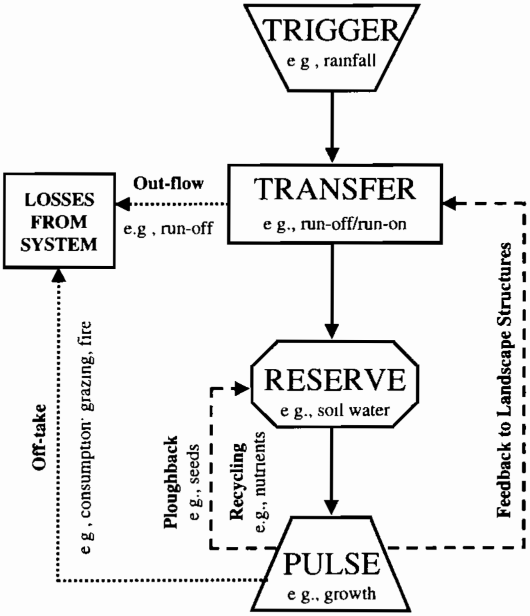

Figure 2.1. The trigger-transfer-reserve-pulse framework for how semiarid landscapes function to trap, store, and recycle limited resources. (Adapted from Ludwig and Tongway 1997; Tongway and Ludwig 1997a.)

a small rainfall event was added to the rain falling on a specified place, more frequent responses to rain, and hence enhanced production would result in that place (e.g., a vegetation band).

To apply this principle to landscapes, zones of runoff and runon need to be identified. The analysis of landscape function can be made on the basis of processes affecting resource transfers acting in space over time. A balance-sheet approach is possible with respect to limiting resources, so that a well-functioning landscape as a whole has low net loss of resources but high internal redistribution capacity (chapter 5, this volume). By contrast, a landscape with a poor functional status would have high net loss and low internal redistribution. Tongway and Ludwig (1997b) used the concept of a continuum of functionality from "fully functional" to "totally dysfunctional" to describe the ecological status of how well landscapes are working to conserve limited resources.

Banded landscapes lend themselves to this type of analysis because of the abrupt boundaries between their component parts (at landscape scale). There is a clear discrimination between the runoff-runon zones in a resource source-sink sense (Tongway and Ludwig 1990; Ludwig and Tongway 1995) and the major differences in hydrological performance in the respective zones (Greene 1992; chapter 5, this volume). That is, the efficiency of resource mobilization and capture is simple to assess, compared with other landscapes where pattern is more cryptic. Modeling these processes is eminently feasible and applicable to scenarios of degradation. These are discussed in detail in chapter 8 of this volume. This approach is also in accord with the notions of landscape patchiness elaborated by Forman and Godron (1981), who identified five patch types according to the cause of their initiation. Banded landscapes clearly fall into their classification of "environmental resource patch," which invokes the overtly spatial transfer of resources into the patch.

Banded Landscapes in the Context of Ecological Heterogeneity

Concepts in ecological heterogeneity have developed over the past four decades to account for innumerable examples of spatial and temporal biological variation. Kolasa and Pickett (1991) have elaborated a wide range of definitions of patches, boundaries, and examples of heterogeneity and its detection for many circumstances from a number of sources (chapter 3, this volume). Heterogeneity per se is so ubiquitous in nature that it needs to be narrowed down to the context of its application.

Many examples of heterogeneity theory are being developed to detect diffuse boundaries and identify temporary or disaggregated pattern elements, particularly in systems in which heterogeneity varies with the scale of measurement (Kotliar and Wiens 1990). However, the consideration of banded landscapes requires a pragmatic selection of concepts based on the demonstrated reality of the pattern and the hypotheses needing to be tested.

Banded landscapes should be viewed as examples of *functional heterogeneity* whereby pattern elements are linked by processes mediated by environmental gradients acting at the scale of the patch (Kolasa and Rollo 1991). This has clear links with the patch system described by Forman and Godron (1981).

Summary

In this chapter we answered five basic questions about banded landscapes by reference to the literature: (1) why do they form? (2) how are they maintained? (3) how do they move? (4) how do they work to conserve resources? and (5) how do they fit within heterogeneity theory? The accepted paradigm is that banded vegetation forms on landscapes with gentle slopes where soils of low infiltration capacity leads to runoff as overland sheet-flow. Bands form when obstructions to this flow trigger positive feedback mechanisms to deposit sediment and absorb water so that vegetation develops in the form of an arc. The theory that we accept to explain the maintenance of banded landscapes is that once vegetation bands form, their capacity to obstruct slow sheet-flow is improved, so that sediments and organic matter are continually being deposited within the bands, thus maintaining them. An organic matter/bioturbation subprocess serves to augment the runoff-runon processes. The hypothesis best explaining the movement of vegetation bands upslope is again related to how they obstruct flows. At the immediate upslope edge of a vegetation band, water flow slows, sediments and litter drop out, and the infiltration of water increases. This favors the upslope germination of pioneer plants in this upslope edge, with death perhaps occurring due to resource starvation at the downslope edge; thus bands move upslope. A generic framework of how banded landscapes function to conserve limited resources, based on the Noy-Meir source-sink theory, was also presented, together with fitting banded landscapes into generic theories of ecological heterogeneity. In discussing all these theories and frameworks, we attempted to link past and recent research, all triggered by our fascination with banded landscapes.

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3. Specific Methods of Study

Josiane Seghieri and David L. Dunkerley

Introduction

Banded vegetation is composed of two interacting and interdependent "phases": a vegetated phase and a more-or-less bare phase. Both phases are oriented along the contours and alternate along the main slope. As an array of bands in a landscape, the product is a system operating to display unique larger functional properties (Archer and Smeins 1991). The bare (or sparsely covered) soil zone acts as an impluvium because it generates a high proportion of runoff (Peugeot et al. 1997). The densely vegetated zone downslope (runon or sink area) intercepts and absorbs runoff water due to high infiltration rates (Delhoume 1992; Green, Kinell, and Wood 1994; Galle, Ehrmann, and Peugeot 1999). The two combined phases constitute the basic functional unit of the banded landscape, repeated many times across the landscape.

In Africa, banded landscapes have been reported from Mauritania to Somalia and Sudan (Macfadyen 1950; Clos-Arceduc 1956; Boaler and Hodge 1964; White 1970; Wickens and Collier 1971; Boudet 1972; Lawesson 1990; Leprun 1999). They have also been studied in Mexico (Cornet et al. 1992) and Australia (Slatyer 1961; Mabbutt and Fanning 1987; Ludwig and Tongway 1995).

In banded landscapes, structure and function are particularly strongly linked, but they can be affected by stress or disturbance, either from their natural environment (e.g., drought) and/or from human pressure such as grazing pressure or wood harvesting (chapter 11, this volume). It is the objective of this chapter to discuss some potentially useful field procedures and data analyses to address the four most frequently asked questions about banded landscapes:

- What is the geomorphological context of their occurrence?
- What is the fine-scale structure within the bands and its variation in space and time?
- What are the dominant biotic and abiotic properties and processes involved?
- Do the vegetation bands move upslope over time?

Banding is a simple, clear-cut example of ecosystem heterogeneity. Consequently, many methods developed to study heterogeneity in landscapes generally are useful in banded landscapes (Whittaker 1975; Greig-Smith 1983; Forman and Godron 1986; Turner and Gardner 1990; Kolasa and Pickett 1991; Dale 1999). The vegetation bands are sometimes asymmetric: the boundary of the upslope edge tends to be sharp, whereas the downslope edge tends to be more diffuse. In terms of resource distribution, this corresponds to a sharp increasing gradient in resource availability from the upslope edge to the core and the reverse extending from the core to the downslope edge. Vegetation structure mirrors this. Most of the methods used to detect, locate, and analyze ecotones or boundaries from ground-level survey data can be used (Forman and Godron 1986; Ludwig and Cornelius 1987; Johnston, Pastor, and Pinay 1992). The second section discusses some useful ground-based methods of data collection and the most appropriate spatial statistical analyses to assess the pattern properties in banded landscapes.

Understanding the processes by which the landscape transfers, accumulates, and uses its vital resources is of considerable importance in understanding overall function (Tongway and Ludwig 1997). Hydrological processes have been recognized as driving and controlling the structure and the dynamics of the vegetation at different spatial and temporal scales (chapters 4 and 5, this volume). Different ways to assess and to verify these, mainly hydrological, processes involved are summarized in the third part of this chapter.

Upslope migration of vegetated patches was often presumed or deduced from the spatial organization of the biota and the inferred runoff/runon processes in action (Ambouta 1984; Cornet et al. 1992; Montaña 1992; Mauchamp, Rambal, and Lepart 1994; Thiéry, d'Herbès, and Valentin 1995). Positive proof has not been forthcoming in the period these landscapes have been studied, and the issue is still being scrutinized. Methods used to address upslope migration are reviewed and considered in the fourth section.

Coarse-Scale Observations and Analysis

The first distinct feature of banded vegetation ecosystems is that most of the heterogeneity of the pattern is expressed in the horizontal plane. The first investigators recorded the distinctive pattern from aerial photography (Ives 1946; Macfayden 1950; Clos-Arceduc 1956). They were able to use this imagery to derive information on patch density, size, shape, edge morphology, location, and spatial distribution of bands in the landscape (e.g., more or less random, regular, or aggregated). They proposed some causes for the occurrence of banded landscapes. Ives (1946) related pattern orientation to the dominant wind direction, whereas Clos-Arceduc (1956) observed that the bands were parallel to the terrain contours.

More recently, remote sensing allowed quantification of the structure from digitized photographs (Mougenot and Hamani 1997; Wu, Thurow, and Whisenant 2000). Digitized aerial photographs have had limited use until now, although substantial future developments are expected as pixel size becomes smaller and image registration becomes more reliable. Valentin and d'Herbès (1999) associated broad-scale banding character with a rainfall gradient, comparing different sites along a latitudinal transect. Jacqueminet and associates (1989) characterized the class distribution of vegetated patch size on a binary picture. Couteron (1998) used spectral analysis by a Fourier transformation (Mugglestone and Renshaw 1996) to compare the periodicity and the dominant orientation of more-or-less banded vegetation landscapes. Also, a model based on the interplay between short-range cooperative interactions and long-range self-inhibitory interactions inside the vegetation community has been calibrated with the Fourier transform of a digitized aerial picture of a banded landscape in Burkina Faso (Lejeune, Couteron, and Lefever 1999; chapter 9, this volume).

Remotely sensed images from aircraft or satellites provide information on spatial or temporal changes in patch configuration through multisite or multidate analysis (White 1969). They allowed investigators to characterize, classify, and quantify patch cover over time at coarse scale. Recently, more attention has been paid to coarse scale as new analytical techniques are developed, and the need to follow trends over time increases in response to climatic or anthropic stress (Couteron 1998; Wu, Thurow, and Whisenant 2000). The task for future investigations is now to fill the gap between local field observations and data from remotely sensed imagery to establish an unbroken information continuum between the different scales (Bastin et al. 1993). Indeed, there is an urgent need to extrapolate ground-based interpretation to coarser scales and test cross-scale relationships.

Ground-Based Characterization and Quantification of the Pattern Properties

Data Collection

Grid surveys provide the most rigorous technique for the collection of data to characterize and quantify the heterogeneity of patterned landscapes. The resulting "map" of the landscape enables the two-dimensional character to be appreciated and provides incontrovertible proof of banding. Although useful for both symmetric and asymmetrical internal band structure, grid surveys require big data sets and need more complex data manipulation for landscape analysis. It is thus somewhat more costly in the expenditure of time, effort, and measuring equipment than simple transects (Tongway and Ludwig 1990; Cornet et al. 1992; Montaña 1992).

The linear transect, a special case of the grid, enables the collection of parameters or variables reflecting spatial changes in banded vegetation with economy of time and effort. The most widely used transect type in banded landscapes is the gradient-oriented transect ("gradsect") specifically aligned to reflect the effect of the strongest environmental gradient (Gillison and Brewer 1985; Ludwig and Cornelius 1987). In the case of banded vegetation, the gradsect crosses the vegetated bands from upslope to downslope. Most of the complexity of the biotic and abiotic features in banded landscapes can be revealed on such gradients. Gradsects are effective in providing data relating ecological features to causal physical processes and establishing spatial connectivity in the landscape due to the distributive flows of water, sediments, dust, nutrients, propagules, and so on (Tongway and Ludwig 1990). More generally, gradsects are the basic method of data collection to quantify ecotones (Johnston, Pastor, and Pinay 1992) because they are amenable to a variety of vegetation patch shapes.

There are many variations of gradsects in practice. They can be linear with point or segment data (Slatyer 1961), or in the form of a belt, using quadrat data (Ludwig and Tongway 1995; Couteron, Mahamane, and Ouedraogo 1996). Gounot (1969) used the segment method along linear transects to assess foliar cover and thus obtain the comparative cover and/or biomass of each group of plants. Different widths of transect have been combined (Montaña, López-Portillo, and Mauchamp 1990; Mauchamp et al. 1993). Couteron and colleagues (2000) used quadrats of two sizes along the same transect to measure the density of plants of widely different abundance. This practice enables economy in data collection effort.

Lateral variation within vegetation bands can be studied with transects oriented on the contour, where heterogeneity is much less pronounced than with gradsects (Worral 1960a; Boaler and Hodge 1964; Montaña, López-Portillo, and Mauchamp 1990). Erhmann (1999) studied differences of structure and function between convex and concave boundaries alternating along the upslope boundary of a thicket. She compared these data with the vegetation distributions in gradsects oriented down the slope, crossing the thicket.

Transects are flexible enough to permit the collection of data at a range of time and spatial scales ranging from small to large (Delcourt and Delcourt 1992). The technique has been used at local scales such as one-patch or across-patch boundaries (Montaña, López-Portillo, and Mauchamp 1990; Cornet et al. 1992; Seghieri et al. 1997). It has also been used to understand linear data dependence on the repetitive pattern (Ludwig and Tongway 1995). In this case, the sampled area must be sufficiently large to include repetitions of the basic functional elementary unit a sufficient number of times (Tongway and Ludwig 1990; Ludwig and Tongway 1995; Couteron, Mahamane, and Ouedraogo 1996). A very wide range of ecological data can be collected by using transects as the spatial reference.

Analysis of Spatial Data

There have been few temporal changes or intersite quantitative comparisons of banded landscape pattern reported in the literature (Valentin and d'Herbès 1999;

Couteron et al. 2000; Wu, Thurow, and Whisenant 2000). Frequently, only descriptive information was provided, and various visual criteria were proposed but rarely defined. Statistical tests are essential to explore detailed questions about pattern (Keddy 1991). We therefore focus here on the statistics of spatial data to analyze banded vegetation pattern.

Several statistical tests of varying complexity are available for spatial data analysis that have been elaborated in a number of standard texts. Cormack and Ord (1979), Greig-Smith (1983), and Sokal and Rohlf (1995) concentrate on the statistical analysis per se, whereas other works focus on the application of spatial statistics to general ecological problems such as landscape ecology (Turner and Gardner 1990), heterogeneity (Kolasa and Pickett 1991; Dale 1999), or landscape boundary detection (Hansen and Di Castri 1992). Few of these were developed specifically for banded vegetation. Statistical analysis of data derived in banded landscapes was a major component in Montaña (1992), Mauchamp and co-workers (1993), Ludwig and Tongway (1995), and Couteron, Mahamane, and Ouedraogo (1996). Despite spatial analysis being able to confirm nonrandom population distributions, the ecological interpretation was not always clear (White 1971; Couteron et al. 2000).

The scope of spatial statistics is too large to be comprehensively reviewed in several pages, nor is it the aim of this chapter. The following section reviews some examples of the main types of spatial statistical procedures that have actual or potential use for banded vegetation analysis. The choice of method depends on the nature and quality of the field data, the ultimate use of the results, and hence the balance between information accuracy and interpretation complexity. Table 3.1 summarizes spatial statistical analysis developed above according to the needs.

Quantification of the Structure Scale

Assessing the scales at which every component exhibits patchiness is crucial to a good understanding of ecological processes and resource utilization (O'Neil et al. 1986, 1988; Pickett et al. 1989; Wiens 1989; Gosz 1993). Despite the obvious

Table 3.1. Classification of Some Spatial Statistical Techniques According to Their Efficiency for a Given Aim[a]

	Quantification of structure scale	Location of boundaries	Delineation of homogeneous areas
Blocking	++		
Autocorrelations/ cross-correlations	++		
Global ecotone detection	+	++	+
Local edge detection (edge detection filters)		++	+
Smoothing filters	+	+	++

[a] Useless if nothing, + can be used, ++ useful

repetitive structure of tiger bush, not all species contribute to the same extent to the pattern perceived at coarse scale. Several species have been noted as taking little or no part in banded pattern. This is the case of *Prosopis glandulosa* in Mexico (López-Portillo and Montaña 1999) and *Pterocarpus lucens* in Burkina Faso (Couteron, Mahamane, and Ouedraogo 1996). The techniques described in this section enable the size and periodicity of the repetitive pattern to be characterized with statistical rigor and to determine which variables contribute to pattern.

Greig-Smith (1952) proposed a "blocking technique" that originally used field data derived from a grid of contiguous quadrats. Kershaw (1957) later adapted the method for use on linear transects. In this procedure, field data from a pair of contiguous quadrats are grouped into a block. All other quadrats are treated similarly. These blocks in turn are grouped, pairwise, into another set of larger blocks. This grouping process continues until only two blocks remain, each containing one half of the total data set. This creates a nested hierarchy of block sizes, with respective means and variances calculated at each block size. An analysis of variance is then performed for each block size in the hierarchy of blocks, the variance being partitioned between and within block size. The relationship between block size and mean square variance is then plotted, resulting in peaks and troughs emerging. Peaks correspond to block sizes in which adjacent blocks are dissimilar, whereas troughs represent block sizes in which adjacent blocks are similar (Goodall 1974). Although being criticized, mainly because the "treatments" are not independent as they should be in analysis of variance, the technique underwent a number of improvements (Ludwig and Goodall 1978; Turner et al. 1990).

The development of statistical tests to determine whether the spatial distribution of organisms along a resource gradient deviate significantly from random distribution led to the use of techniques that partition variance into spatial lags (Turner et al. 1990). For example, an autocorrelation test can be applied to see whether the observed value of a variable at one location is significantly dependent on values of the same variable at other locations. It assumes that the variables are normally distributed (Sokal and Oden 1978). This approach has the advantage that the locations as well as the attributes of data points are taken into account. Autocorrelation is suitable for parameters whose value varies at local scale. It does not account for regionalized variables that are too irregular to be modeled by smooth mathematical functions (Johnston, Pastor, and Pinay 1992). Repetitions of sequence are found by computing a measure of self-similarity in the data. The one sequence is compared at successive positions, as in the moving window technique. The degree of similarity between adjacent parts along the transect is computed, and every point is compared with every other to reveal the positions of strong similarities. These methods require large data sets and need very consistent autodependencies within the data sets to be powerful discriminatory tools (Ludwig, pers. comm.). Thus, it is appropriate for use in banded vegetation in which autodependency is expected. Other techniques that partition variance into spatial lags were presented by Turner and associates (1990). Cross-correlation has been applied to Mexican banded vegetation (Mauchamp et al. 1993) and semivariograms for regionalized variables in Burkina Faso (Couteron, Mahamane, and Ouedraogo 1996). The relative contribution of different shrub species to the banded pattern was thus verified. Dominant species were found to contribute the most to the banded pattern but not all the others.

Parameters of banded pattern based on periodic functions such as Fourier analysis (Renshaw and Ford 1984) have been used in Burkina Faso (Couteron 1998). This approach is particularly useful in comparing different banded landscapes or the distribution of various components within the same site because of the strong periodicity of the vegetated bands. This periodicity is conventionally thought to be the result of the dynamic balance between functional properties of vegetation and abiotic factors. One can test whether given components actually contribute to the overall periodicity measured by applying a Fourier analysis to each component. This is helpful, for instance, to address the role of the biological factors on the natural maintenance of the pattern or in discussing the effect of management on landscape function.

Detection and Location of Boundaries Between Pattern Elements

The location of boundaries between contiguous elements of banded pattern needs to be determined objectively and quantitatively to compare the pattern on different sites or on the same site over time. Location of the boundaries can be addressed through three types of method.

1. *Optimal limits.* Godron (1966) described an analysis based on the information theory using species presence along a transect to define boundaries in terms of "optimal limits." The method involves the use species presence/absence data on consecutive points, segments, or quadrats along a transect, the calculation of a relative value of heterogeneity ("information") for each species at each transect location. The heterogeneity value is plotted against the location on the transect. The optimal limit occurs where this heterogeneity value is at a maximum. The calculation can be computed for one, several, or all the species recorded. An analysis of the species distribution along the transect in relation to the "optimal limit" location gives the relative contribution of each species to the limit. This method has not been tested yet on banded vegetation patterning but was used on a less markedly heterogeneous pattern in a wet savanna in the Ivory Coast (Godron and Bacou 1975). "Global zonation" is a similar approach that also searches for edges in blocks of data by breaking the whole transect into segments that are as internally homogeneous as possible and as distinct as possible from adjacent segments (Davis 1986). Turner and co-workers (1990) discussed this method in some detail in relation to the quantification of landscape heterogeneity in general. Global zonation makes no assumptions about the repetitiveness of a pattern but is applicable to landscapes with abrupt transitions. It assumes that the landscape is composed of discrete homogeneous patches of any size. This makes it a useful spatial statistic to be applied to banded vegetation and also to other vegetation patch types (chapter 1, this volume).
2. *Edge detection filters.* This method is simple but powerful and useful in the analysis of ecological discontinuities (Niblack 1986). A moving split window

is laid over equal numbers of equally spaced sampling units, and an index of similarity or dissimilarity is calculated at each location of the window center (Ludwig and Cornelius 1987; Johnston, Pastor, and Pinay 1992). It permits the detection of landscape boundaries from one-dimensional data or to locate positions of high heterogeneity. It consists in calculating the "dissimilarity" (i.e., statistical distance) between values of a given attribute on either side of a moving split window of arbitrary width (Ludwig and Cornelius 1987). The approach is now in common practice (Turner et al. 1990; Kolasa and Pickett 1991; Johnston, Pastor, and Pinay 1992). The dissimilarity between attribute values of two parts of the split window is calculated at each location and computed successively along the entire transect length. A boundary is signaled when maximum values of the "statistical distance" metric occur. This indicates that the rate of change of the landscape attribute is at a maximum or peak. When these values are plotted against the respective positions on the transect, the location, the physical width, and "strength" of the boundaries are displayed. High and narrow peaks represent abrupt boundaries, whereas wider and lower peaks characterize more diffuse boundaries (Ludwig and Cornelius 1987; Johnston, Pastor, and Pinay 1992). The analyst can alter window widths at will to look at landscape organization at different scales. The ultimate quality of the boundary analysis depends on the resolution of the data used and the innate characteristic variation in the attributes involved (Turner et al. 1990). For assessment of band boundaries in banded vegetation, Ludwig (pers. comm.) used first a window width as small as possible (although this generates a plot with quite a lot of "noise"). He then slowly increased the window size until distinct peaks, denoting the landscape pattern elements, emerged from the noise. Too large a window as a first choice might have "smoothed" the analysis excessively. Johnston, Pastor, and Pinay (1992) used the method to locate and to assess the stability of the location and of change in several soil water attributes in Minosota. Ludwig and Tongway (1995) used it to assess the spatial organization and the functional connectivity in Australian landscapes of varying pattern clarity. A wide range of ecological data may be used as the input data.

3. *The "median smoothing filter"* is a method somewhat the reverse of the second approach (Niblack 1986). It consists in using a moving split window to locate homogeneous vegetated patches instead of to locate the position of maximum heterogeneity. Couteron and colleagues (2000) used it to compare two African banded landscapes differing only in the soil properties. They compared the thicket sizes and spatial distribution between a banded landscape in Burkina Faso and another one in Niger. A thicket was defined as "a stretch of consecutive quadrats for which the proportion of quadrats occupied by at least one mature woody plant is 'sufficiently' high." Variables used, such as plant "maturity," the size of the moving window, and the threshold of frequency of occupied quadrats in each window were defined from an existing knowledge of species growth and of coarse pattern nature. This smoothing technique does not alter the location of the boundary. It is especially useful when boundaries are not distinct.

Processes Within the Structure

Most of the biological processes such as seed dispersal, plant recruitment, competition, succession, role of soil microfauna, predation, and their spatial relationships within and between general patched vegetation can be found in Forman and Godron (1986) and Forman (1995). Most of the biological processes have not yet been extensively studied in banded vegetation patterns (Mauchamp 1992; Mauchamp et al. 1993; Couteron, Mahamane, and Ouedraogo 1996; Ouedraogo 1997; chapters 6 and 7, this volume). However, they were recognized as being important factors in maintenance and regulation of hydrological processes (runon, infiltration) and in the capacity of banded landscapes to conserve resources and biological and soil processes (Greene, Kinell, and Wood 1994; Tongway and Ludwig 1996; Ludwig et al. 1997).

Runoff and runon processes, which are crucial in banded landscapes, are the result of different infiltration rates in the " source" and "sink" areas, respectively. Runoff transfers water, soil, and litter from the source area, and infiltration and deposition processes recharge the fertile areas (Tongway and Ludwig 1997).

Quantification of the Local Water Balance

In arid and semiarid environments, consistent differences in available soil moisture are one of the main causes of the spatial heterogeneity of the landscape (Yair and Danin 1980; Olswig-Whittaker, Shachak, and Yair 1983). High infiltration in the vegetated band is responsible for establishing and maintaining vegetation pattern, as well as controlling the dynamics of the structure and its components by providing water for plant growth (chapters 5 and 7 to 9, this volume). To establish and quantify the efficiency of vegetation bands in intercepting, storing, and conserving water, the measurement of infiltration processes is fundamental. This is true both in the short term, in terms of resource supply to living organisms, and in the longer term and at coarser scales when dynamics and stability of the entire landscape structure were considered (Ludwig and Tongway 1997). An overview of the advantages and disadvantages of most of the techniques used to measure soil moisture content is described in Noble (1973). We discuss below the techniques that have been already used in banded landscapes.

Direct Measures

Monitoring the soil moisture content directly in different landscape pattern elements provides concrete verification of differential infiltration processes. The measurement locations (generally along a transect normal to the contour lines) and recording frequency need to be appropriate for the space and time scales being specifically addressed. Gravimetric techniques, and after calibration, neutron or gamma probes and time-domain reflectometry (TDR) all record the soil water storage in different soil layers. TDR measures volumetric water content absolutely. It is restricted to shallow depths as the measuring nods are delicate and easy to distort. The neutron probe is probably the technique the most used in tiger bush sites

(Delhoume 1992; Greene, Kinell, and Wood 1994; Peugeot et al. 1997; Galle, Ehrmann, and Peugeot 1999). The advantage of this technique is that once an access tube is properly installed, there is no further disruption of the soil and moisture content can be recorded as frequently as required. Repeated gravimetric sampling tends to destroy the site or at least alter the characteristics. The most suitable measurement regime is one in which the intervals between readings gradually increase after the rainfall event and the soil moisture decreases (Galle, Seghieri, and Mounkaïla 1997; Seghieri et al. 1997; Galle, Ehrmann, and Peugeot 1999; Seghieri and Galle 1999). However, the quantitative evaluation of the water status in the soil can be deduced only if appropriate calibration has been undertaken (Noble 1973).

Indirect Measures

Methods of measuring the water potential, which is directly linked to moisture status, are essential to study the water–soil–plant relationships and the derivation of moisture retention curves. In the field, one of the main tools in assessing water stress in plants is by measuring water pressure with a psychrometer or a pressure chamber (Seghieri and Galle 1999), and in the soil, tensiometers are commonly used (Peugeot et al. 1997). However, measuring water tension gives indirect measure of the reserves of the soil water storage because of the large changes in potential occurring at very short time distance intervals. Rather, it characterizes the potential transfers of water within the continuum soil-plant-atmosphere (Noble 1973). Soil tensiometers need to be buried in the soil, and the excavation of the soil types commonly found in tiger bush is extremely hard. The size of the soil samples required, to be representative, is large. Indeed, large stone fragments mainly located in the runoff zone and macropores located in the thicket center, create preferential flow paths (Bouma and Dekker 1981; Laurent et al. 1988; Ritsema and Decker 1996). In addition, the soil is generally hard to dig despite extreme variations of the soil resistance found by Dunkerley and Brown (1999). Those authors showed 400% change in soil unconfined compressive strength, measured in kilo-Pascals (kPa). It ranged from peaks of 4,000 kPa, immediately upslope of thickets on a hard setting duplex soil, to an average of 500 kPa within the thickets less than 10 m away on a self-mulching clay.

Other techniques, such as electrical, thermal, acoustic, or cohesive properties of the soil, measure water indirectly in the sense that they measure or sense some physical or chemical properties of the soil that is dynamically related to changes in soil moisture (Noble 1973; Valentin, d'Herbès, and Poesen 1999).

Runoff assessment

Runoff-runon processes caused by differential infiltration rates in landscape zones has long been recognized as the primary controlling factors of banded vegetation patterning (Worrall 1959; Slatyer 1961; Boaler and Hodge 1962, 1964; White 1969; Wickens and Collier 1971; Ambouta 1984; Tongway and Ludwig 1990; Cornet et al. 1992; chapter 4, this volume). Runoff-runon flows also mediate erosion/deposition processes between "source" and "sink" zones (Ludwig et al. 1997).

Although there was general acceptance of the runoff-runon proposition, there are relatively few studies in which the nature of the runoff flow was observed and described (Boaler and Hodge 1964). Barker (1992) used drops of dye to study flow patterns of sheet runoff during rain and observed diffuse thin flow moving at about 0.5 m s^{-1}, with low stone and sediment transport. He also noted that when water flow was confined in rills (on a degraded part of his site), the velocity increased by fourfold, compared with the sheet-flow, easily transporting stones weighing up to 80 g. Recently, studies by Greene (1993), Greene, Kinell, and Wood (1994), Peugeot et al. (1997), and Galle, Ehrmann, and Peugeot (1999) measured the runoff flow rates from bounded runoff plots (100 m^2 or larger in size) during rainfall events. This technique can be used to measure both water and sediment carried by runoff and is more fully described by Greene, Valentin, and Estève in chapter 4 of this volume. When the plot exceeds 10 m^2, both sheet-flow and channel water flow may be taken into account. The value of this procedure is to measure with some precision the quantity and dynamics of runoff generated from the experimental area. The study plot could examine the behavior of either a bare or a vegetated zone alone or, preferably, the basic functional unit composed of a paired runoff-runon complex. Hudson (1993) noted that these methods measure the total amount of water running off the bounded area but do not necessarily identify the origins of the flow within the plot.

Microplots of 1 or 2 m^2 may be appropriate research tools to characterize and compare the infiltration/runoff potential of different locations within a banded landscape complex, relating the data to different soil surfaces (e.g., different soil crust types). The method is relatively inexpensive, and multiple replications are possible. The use of rainfall simulators on such quadrats enables the use of controlled rainfall characteristics (e.g., intensity and duration) and also to collect data in dry field conditions (Mauchamp and Janeau 1993; chapter 4, this volume). However, runoff data (and sediment yield if desired) is interpretable only at the scale of the plot: scaling the results up to quantitatively represent whole landscape performance is not possible due to nonlinearity in the relationships when going from fine to coarse scale. Data from small plots tend to overestimate erosion measured at landscape scale. However, these methods are useful in making intersite comparisons or comparing the same site over time.

In most of these studies, the plots have specifically installed barriers or boundaries to confine runoff and define the area from which the runoff and soil are being collected, but there are some cases in which it is appropriate to use unbounded plots (Planchon 1991). They used a small collecting gutter, let into the soil surface and oriented on the contour, and connected to a collection container on the downslope side. This arrangement permits the measurement of the amount of water crossing a watershed section defined by the width of the gutter after each rainfall event. The gutter length must be chosen to represent the average distance between plants likely to intercept runoff flow (Planchon and Janeau 1990). Various degrees of refinement are possible with this approach, but often a simple design yields adequate data. The method requires and is amenable to multiple replications to overcome the uncertainties arising from the lack of plot boundaries and to account for site variations in terms of microtopographic features and rills (Barker 1992). This technique was used in banded vegetation in Niger to evaluate the rainfall conditions (intensity and amount) under which the runoff can cross the thicket (Ehrmann 1999).

Casenave and Valentin (1992) used an indirect technique that classified soil surface crust types into groups representing a range in runoff capability in semiarid areas of West Africa. They showed that it is possible to subdivide the soil surface type into a number of distinct, internally homogeneous hydraulic units, called "unit surfaces." Owing to the large number of possible combinations of these surfaces, the concept of "surface features unit" was defined to characterize a small watershed composed of differing unit surfaces (i.e., a group within which interactions occur), as it is the case in banded landscapes (Seghieri et al. 1997). Mapping the units facilitates modeling of the hydrological behavior of the basic functional unit, when the parameters of runoff production are combined in proportion to the surface area occupied (Janeau, Mauchamp, and Tarin 1999; Valentin and d'Herbès 1999; Valentin, d'Herbès, and Poesen 1999; chapter 4, this volume).

Another indirect technique is to use microtopography to predict the runoff-runon behavior at unit surface scale. At the fine scale, the roughness of the soil is of great significance for the behavior of surface runoff and erosion-deposition processes. It was recently used to characterize surface runoff as one of the many factors that differentiates the various components of the mosaic (Dunkerley and Brown 1999). Tongway (1994) and Tongway and Hindley (1995) used very similar assessments of soil microtopography in implementing routine monitoring procedures for assessing the functional status of banded landscapes in Australia.

Experiments and Techniques Used to Verify the Processes

Some processes have been deduced from description of spatial pattern alone. Keddy (1991) proposed to statistically test the relationships between state variables (e.g., biomass and species richness or competition and biomass) from data describing organism distribution. However, even if the properties of every species were known, they might not allow us to understand and predict the whole system behavior. Relationships between sets of dependent variables relating to organisms (i.e., biomass, cover, density) and state variables relating to resources (i.e., soil water, nutrients, and organic matter contents or seed stock) could be tested or related to soil characteristics (i.e., soil surface features, porosity, infiltrability, hydraulic conductivity). Even so, such relationships tend to reflect past circumstances in a static sense and do not inherently enable a predictive understanding to be developed.

Applied experimental treatments have been helpful to effectively and quickly validate or refine hypotheses and assumptions about landscape function that follow from observations in natural conditions. As an example, in Sudan, Worrall (1960b) anchored palm leaf mats to the ground in the bare soil zone at the beginning of the rainy season to simulate the role of natural vegetation cover in collecting water. At the end of the rainy season, the mats had not only collected more rainwater than the bare ground but also much sand and dust, so that they had become firmly anchored in the ground without the need of stakes. From testing a simple hypothesis about water accumulation, Worrall (1960b) acquired information about other processes such as sediment deposition after a single rainy season. A similar procedure was used at Lake Mere in Australia (Tongway and Ludwig 1996; Ludwig and Tongway 1997; Noble, MacLeod, and Griffin 1997). "Brush piles" on the ground quickly succeeded in trapping runoff water, soil sediments, and litter, thereby creating new fertile patches with greatly improved biological, chemical, and physical soil properties compared with the controls composed of untreated, bare, stony slopes. Experiments, therefore, may achieve faster and more precisely interpretable outcomes due to the specific control of landscape processes than observations of natural processes under ambient conditions. For instance, Mauchamp and Janeau (1993), when using a rainfall simulator, applied concrete to the base of shrubs in banded vegetation of Mexico. They demonstrated the role of the shrub canopy in decreasing the kinetic energy of the raindrops and in creating stem flow that channeled water into the base of the shrub: the lower the rain intensity, the greater the "harvesting" effect, due to less vigorous flow rates Two independent experiments investigated the restriction of runon into vegetated bands. In Niger, Seghieri and Galle (1999) built a wall at the upslope boundary of a thicket to restrict runon. Responses in terms of infiltrated water, vegetation phenology, and physiology were assessed. Differential responses from distinct zones and species were found. The experiment verified the necessity of the runon water, quantified its benefit to the vegetation, also showing that the gains were spatially heterogeneous. In Australia, Noble, Greene, and Müller (1998) prevented runon water infiltration in replicated plots in the interception zone by sheet metal barriers buried in the ground, with 30 cm exposed. They recorded a severe inhibition of the herbage dry matter production (see Figure 11.2, this volume). The requirement for upslope runoff to sustain downslope vegetation had been widely accepted in principle before this work, but its significance had not been experimentally demonstrated. Keddy (1991) advocated an experimental approach to verify the presence of particular trends in those processes and their constraints or boundary conditions.

Dynamics of the Banded Vegetation Patterns

A review of the accumulated knowledge on vegetation dynamics in banded patterns is given in chapter 7 of this volume. Temporal changes are affected by both natural (mainly climatic) and human influences (grazing, wood harvesting), sometimes in combination with a synergistic effect on the landscape. Some studies analyzed the status of the ecosystem as consequences of human activities but without monitoring the temporal changes per se (Orr 1995; Achard 1997). A new and effective methodology enabling the long-term survey of the dynamics of the vegetation bands at the whole landscape scale has been reported in Wu, Thurow, and

Whisenant (2000) in Niger. It is based on the quantitative comparison of remotely sensed images, seeking evidence of landscape fragmentation. This study showed that serious fragmentation of the vegetated bands occurred between 1960 and 1992 and that only small increments of band were evident. These increments only occurred on the upslope edge of the band, and no evidence of "defragmentation" or lateral extension of the bands was found.

Upslope migration of the vegetation bands is one of the most debated questions about the long-term functioning of banded landscapes. Evidence and predictions of both movement and refutation of the possibility of movement are common in the literature (chapter 2, this volume). As the detailed studies of banded landscapes have been over only short time spans, evidence of either movement or stationarity may well be confused by inadequate data to properly support either position. For example, movement may be part of a cyclic expansion-contraction phenomenon ("pulsation"), driven by cyclic variations in rainfall. Consequently, techniques to rigorously verify (or deny) migration and then to measure the rate of movement over long time scales are required to ascribe more certainty to this controversy.

Direct Measures

Ground benchmarks are the most direct technique to check whether movement (either migration or pulsation) of the vegetated patches can be measured and the rate estimated. This was done by Worrall (1959) for annual grass bands in Sudan (0.3 to 1.5 m yr^{-1}) and by Leprun (1999) for upslope expansion in Mali (0.1 to 0.75 m yr^{-1}). Cornet and associates (1992) and Montaña (1992) studied migration by using multi-annual surveys of plant population frequency in the upslope and downslope borders of thickets within a grid of contiguous quadrats. They were unable to measure a migration rate in the more than 5 years of their study. Clearly, the time scale of observations should be commensurate with the expected time scale of the system dynamics. It is possible that migration is a stochastic process, depending on climatic or other circumstances not yet clearly defined.

Indirect Measures

Indirect assessments of band movement have largely been concerned with evidence provided by vegetation dynamics inferred from the spatial pattern of seedling/dead trees across the band (i.e., along the resource availability gradient) (Couteron et al. 2000) or by tree age distribution (Mabbutt and Fanning 1987; Tongway and Ludwig 1990; Ichaou and d'Herbès 1997). Mabbutt and Fanning (1987) used the depth of siliceous hardpan to counter propositions of movement. Under the mulga bands, the hardpan was deeper than in the open bare areas, thus providing a larger soil water store for the long-lived mulga trees to use. The spatial distribution of natural isotopes of carbon may provide evidence of the long-past presence of plants in the bare zone and thus be helpful in providing insights into long-term dynamics (Chappell et al. 1999; Guillaume et al. 1999), but the evidence is not yet compelling.

Summary

The literature reviewed here provides a wide range of techniques useful in the study of banded landscapes, ranging from simple to complex, cheap to expensive, and from static to dynamic. Research in banded landscapes has only recently moved on from descriptions of pattern to assembly and response rules (Keddy 1991) to provide a predictive understanding of landscape function and the effects of perturbation. Many of the published studies have addressed simple disconnected aspects of soil physical, chemical, and hydraulic properties and vegetation distribution. Future studies need to integrate these aspects and to address issues such as competition and facilitation processes in a holistic way. This chapter provided an overview of techniques used to date in banded landscapes and refers the reader to concepts and procedures that would facilitate future studies of these aspects.

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4. Runoff and Erosion Processes

Richard S.B. Greene, Christian Valentin, and Michel Esteves

Introduction

Banded vegetation patterning consisting of densely vegetated bands alternating regularly with relatively bare areas of soil is common in many semiarid and arid regions of the world. These areas occur as either woodlands or shrublands in the continents of Australia, Africa, Europe, and North America (chapter 2, this volume). These two-phase mosaics form some of the most important grazing lands in the world. The bands are important areas for primary production, especially on the upward slope from the band. The trees or shrubs in the bands are also important for fuel, as well as providing fodder during droughts.

However, due to a range of factors such as climate change, new and competing land use, and changing social needs, these banded landscapes are coming under increasing pressure (chapter 11, this volume). Even though their existence and some of their characteristics have been well documented over the past 40 years, knowledge about the hydrological functioning of these areas is only now emerging. As a result, they are gradually being degraded. The need to implement this new information is urgent, so that the impact of management does not impinge their long-term viability. Runoff and erosion processes are two of the most important processes determining the long-term stability of these lands because it is likely that sustainable functioning is a delicate balance between appropriate and excessive rates.

The infiltration of rainfall and redistribution of runoff are critical processes in determining the long-term stability of rangelands in arid and semiarid environments. These hydrological processes affect the subsequent spatial variation in available soil water in the landscape and hence have significant effects on diversity and production (Noy-Meir 1973). However, the partitioning of rainfall between infiltration and runoff is difficult to predict with precision. It is mainly controlled by soil surface conditions, especially the nature of the surface crust (Valentin and Bresson 1992) and the amount and type of vegetative cover (Mauchamp and Janeau 1993; Greene, Kinnell, and Wood 1994). Both these types of condition are difficult to quantify, due to significant spatial and temporal variability.

Runoff is also important in rangelands because of its effects on a range of other soil processes. Excessive runoff on sloping land can accelerate soil erosion, as well as enhance processes of nutrient and seed transport from sources to sinks. These processes can have beneficial as well as detrimental impacts on the landscape (Römkens, Prasad, and Whisle 1990). Erosion processes by wind are also important, largely because of their impact on organic matter, seed, and nutrient redistribution in the landscape (Greene et al. 1998).

The aims of this chapter are to

1. outline the occurrence and describe the characteristics of runoff and erosion processes in landscapes with banded vegetation patterns
2. evaluate the role of surface soil characteristics, especially crusting and plant cover, on runoff generation and water harvesting processes
3. draw conclusions about the effects and role of management regulating runoff and erosion processes and hence on the longevity of banded vegetation patterning

Occurrence and Characteristics of Banded Vegetation Patterning

Two-phase mosaics, or banded vegetation patterning (consisting of relatively bare areas alternating with densely vegetated bands), are excellent examples of where the nature of the surface hydrology is directly related to a particular distribution of vegetation. The occurrence of banded vegetation patterning was first recorded in British Somaliland (MacFayden 1950). Since then, these banded patterns of vegetation in woodlands and shrublands have been recorded in several continents, especially in Australia, Africa, Europe, and North America.

Despite regional differences in patterning, they all occur where there is a combination of low total rainfall and sheet flooding processes on medium-textured soils of low permeability (chapter 2, this volume). Sheet-flow mainly originates on bare areas, with excess runoff being shed into downslope bands of dense vegetation, where it is substantially all infiltrated. Laminar runoff is thought to be one key factor involved in the development of banded vegetation (Thiéry, d'Herbés, and Valentin 1995). Changes in surface runoff patterns, and in particular the occurrence of linear flow when rainfall exceeds a certain threshold (685 mm in Niger according to Valentin and d'Herbés 1999), tends to limit the development of long banded patterns (parallel to the contours) and favors the formation of dotted bush (Leprun 1999; Valentin and d'Herbès 1999). However, less than 200 mm rainfall is insufficient for the processes to occur in Mali (Leprun 1999). An optimum rainfall for banded pattern occurrence can be thus defined: nearly 400 mm under Mediterranean semiarid conditions (Spain: Bergkamp, Cerdà, and Imeson 1999), 550 mm under tropical semiarid conditions (Niger: Valentin and d'Herbès 1999), and approximately 300 mm or less in dry semiarid and arid areas of Australia (Tongway and Ludwig 1990; Dunkerley and Brown 1995). These thresholds and optima depend not only on climatic conditions but also on surface soil conditions including surface crusting, degree of roughness, and the amount and type of vegetative cover. The following is an account of the characteristics of banded vegetation patterning in different continents. The effects of surface soil conditions including surface crusting, roughness, and vegetative cover on runoff are discussed later.

Occurrence of Banded Vegetation Patterning in Australia

Banded vegetation patterning occurs in many parts of Australia, mainly in the arid and semiarid zones. Examples are the chenopod (*Atriplex vesicaria*) shrublands in

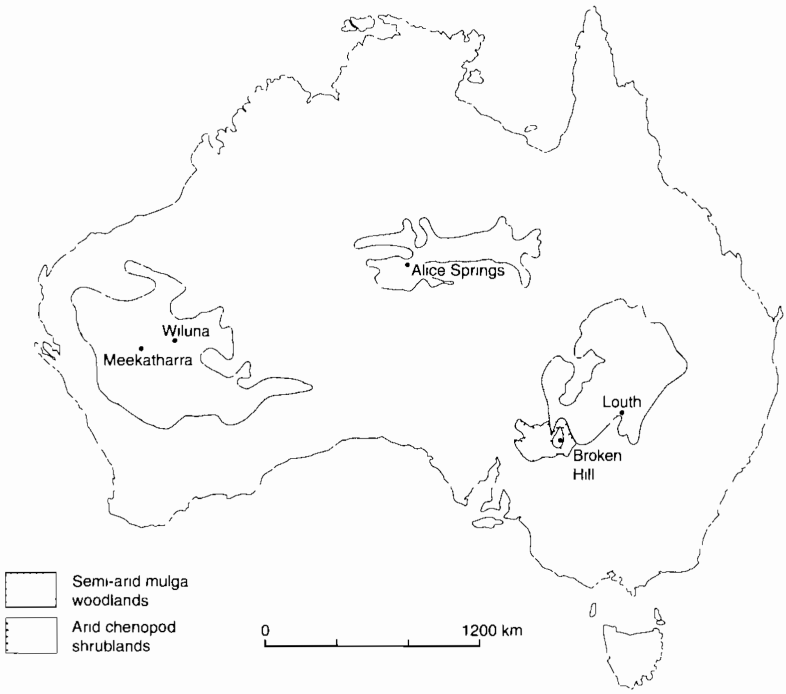

Figure 4.1. Distribution of banded vegetation patterning in chenopod shrublands and mulga woodlands in Australia

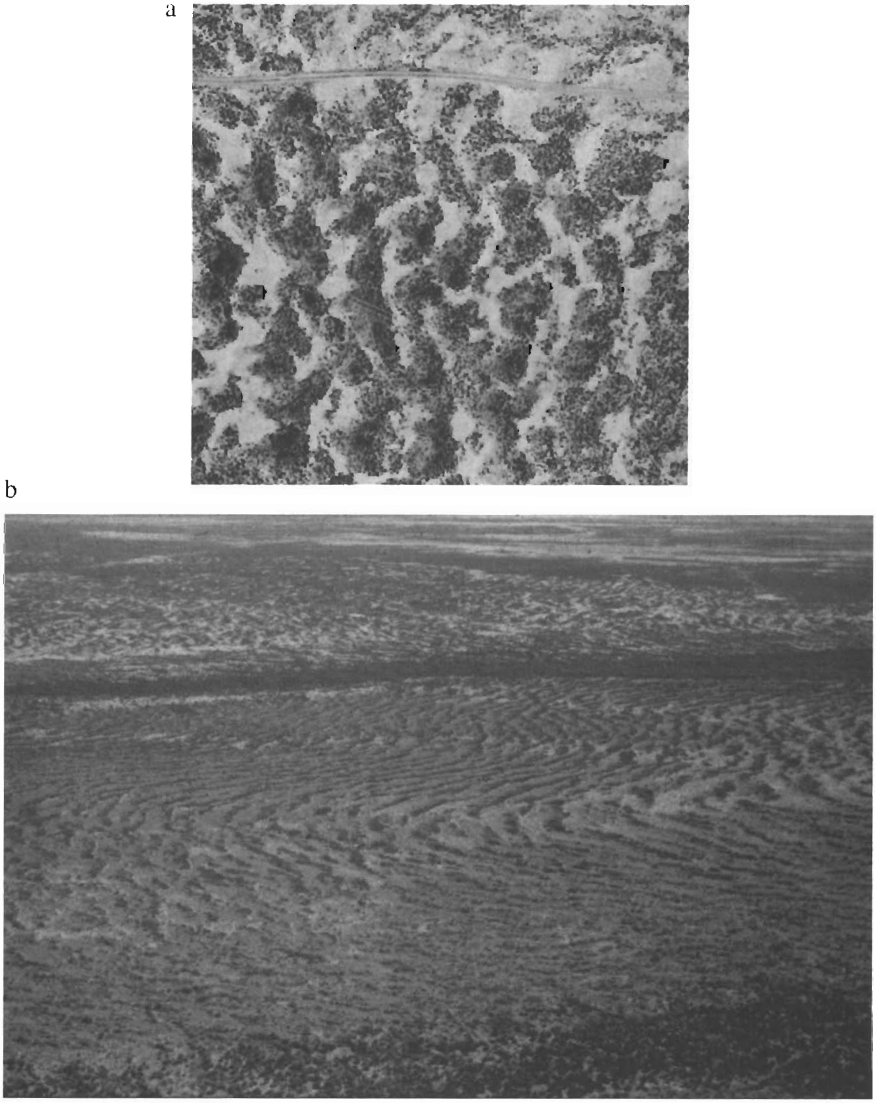

Figure 4.2. Aerial view of banded vegetation patterning. (a) Chenopod shrublands (Broken Hill, New South Wales). (Photograph courtesy of Professor J.A. Mabbutt.) (b) Mulga woodlands (Alice Springs, Northern Territory). (Photograph courtesy of Mr. W. van Aken.)

arid areas of western New South Wales (around Broken Hill) and the northeast of South Australia and the mulga (*Acacia aneura*) woodlands of semiarid areas of eastern Australia (around Louth) and arid areas of Western Australia (Wiluna-Meekatharra) and central Australia (near Alice Springs) (Figure 4.1). Aerial photos depict typical areas of chenopod shrubland (Figure 4.2a) and mulga woodland

(Figure 4.2b), respectively. In Australia, most of the descriptions of banded vegetation patterning have concentrated on mulga woodlands. Banded vegetation patterning in chenopod shrublands has previously been only briefly described by Mabbutt (1972) and Burrell (1974).

Dunkerley and Brown (1995) described in detail the banded chenopod shrublands near Fowlers Gap, New South Wales. The chenopod shrubs are in vegetation bands with intervening bare bands almost completely devoid of vascular plants. However, the soil surface in the bare bands is crusted and veneered with stones. Few surface stones are in the vegetated areas. The main type of patterning is one in which the vegetated areas take the form of isolated patches completely encircled by a bare, gibber-strewn surface. Gibbers are pebbles or boulders (Goudie 1990). These patches are oriented parallel to the contour and are broader in the cross-slope direction than in the downslope direction. Particularly well-developed band patterns that are laterally persistent over hundreds of meters are less common. From aerial photos, it appears that on gentle slopes well-developed banded patterns occur, whereas on steeper gradients, the elongated patch form is dominant.

The first account of banded mulga vegetation in Australia was by Slatyer (1961), who described an extensive area of desert woodland community dominated by mulga (*Acacia aneura*), north of Alice Springs in the Northern Territory (see Figure 4.1). The gradients were less than 0.5% over tens of kilometers, and the mulga was arranged in bands at right angles to the slope. The bands are a kilometer or more in length but only tens of meters wide and are separated by lightly timbered interbands of similar dimensions. The area has an average annual rainfall of approximately 250 mm, with a strong summer maximum. The mulga communities occur on moderately deep, red-earth soils (Stace et al. 1968), which increase in texture from coarse-medium at the surface to medium-fine at about 60 cm.

Another early account of banded vegetation patterning in Australia was given by Litchfield and Mabbutt (1962), who described alluvial wash plains with mulga bands on an interior plateau of Western Australia. The bands were only a few meters across and were sharply demarcated; interbands were several times larger and almost bare. The climate in the region was arid, with a variable rainfall averaging between 200 and 250 mm. The soils were red-earths underlain at shallow-to-moderate depths by an almost ubiquitous siliceous hardpan. The soil depth appears to be greater under the vegetation bands than the bare areas (Figure 4.3).

Mabbutt and Fanning (1987) further described banded vegetation patterning in Western Australia in the Wiluna-Meekatharra area (see Figure 4.1). In this area, there were extensive gentle slopes with gradients between 0.2 and 2%, across which the surface runoff occurs as dispersed sheet-flow or was more concentrated in unchanneled shallow linear depressions or in water lanes. Two main types of vegetation could be recognized in the Wiluna-Meekatharra area. The first type consisted of narrow bands, generally between 10 and 20 m broad and with a band ratio of less than 30%. The second type consisted of broad bands, commonly more than 20 m in breadth and with a band ratio of 30% and greater. The vegetation pattern appeared to be controlled by the depth to hardpan, namely, a greater depth overall in the broad pattern and a marked contrast in depth between band and

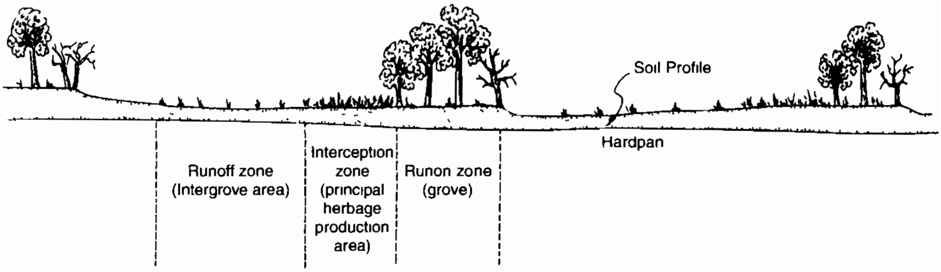

Figure 4.3. Diagrammatic representation of geomorphic sequence in a semiarid mulga woodland.

interband in the narrow pattern (Figure 4.3). The main soils associated with the vegetation banding were red-earths, with a textural range from clayey-sands to sandy-clays.

Banded vegetation patterning in eastern Australia was described in detail by Tongway and Ludwig (1990), who identified and described a patterned sequence of alternating bands and interbands in the semiarid mulga woodlands near Louth, New South Wales (see Figure 4.1). The patterned sequence had three geomorphic zones, each with its distinct vegetation type (Figure 4.3). The zones were as follows: (1) a runoff slope of sparse *Eragrostis eriopoda* savanna (runoff zone), (2) a runon zone of *Monachather paradoxa* grassland at the toe of the runoff slope (interception zone), and (3) a runon zone of *Acacia aneura* woodland (mulga band). The vegetation band–interband patterning in eastern Australia is similar to but differs in detail from such patterns reported for arid and semiarid western and central Australia. The bands in western and central Australia tend to occur on the downslope side of "risers" or on "convex slope-breaks," whereas in eastern Australia such bands occur in distinct "steps" or "flats" in the landscape (Tongway and Ludwig 1990).

Occurrence of Banded Vegetation Patterning in Other Continents

Africa

Vegetation arcs or bands alternating with bare areas are common in arid and semiarid regions of Africa. Clos-Arceduc (1956) first described the so-called *brousse tigrée* (tiger bush) patterned vegetation in Niger. The tiger bush pattern occurs only on the laterite-capped plateaus composed of "Continental Terminal" sandstone with gentle slope (0.2%). The shallow soil is 10 to 100 cm thick over a laterite material and has a sandy clay-loam texture in the upper 60 cm (Seghieri et al. 1997). The woody population is mainly composed of *Combretium micranthum* and *Guiera senegalensis.* The mean annual rainfall of 560 mm of this area and other areas of tiger bush in West Africa is higher than that for other areas of banded vegetation. For example, the mean annual rainfall of areas of vegetation bands in the northern region of Somaliland ranges from 150 to 250 mm, and in southeastern Mauritania, it occurs in a 250-mm rainfall zone (Audry and Rossetti 1962). Worrall (1959) also described grass bands in the Sudan where the annual rainfall ranges from 100 mm in the north to 400 mm in the south.

North and South America

Two-phase mosaics consisting of dense vegetation bands (with the main axis parallel to contour lines) alternating with relatively bare spaces have also been reported in the Chihuahuan Desert in Mexico (Cornet, Delhoume, and Montaña 1988; Montaña 1992). The bare areas consist of an open scrub community with vegetation cover generally less than 5%, whereas the vegetation bands are dense, mixed herb-scrub communities with a cover of approximately 100% (Montaña, López-Portillo, and Mauchamp 1990). The main herbaceous perennial is *Hilaria mutica,* and the two most common woody species are *Prosopis glandulosa* and *Flourensia cernua.* The annual rainfall is 264 mm, 71% of which comes in summer showers of high intensity (López-Portillo, Montaña, and Ezcurra 1996).

Similarly, banded patterns have been investigated in a *Nothofagus betuloides* primeval forest from Bahía del Buen Suceso, on the eastern edge of Tierra del Fuego Island (Argentina). The mean annual rainfall is 600 mm, and the bands are orientated perpendicular to the prevailing wind direction, with older and dying trees in the windward edge and a seedling regrowth in the lee side of each band (Puigdefábregas et al. 1999).

Europe

The only published studies on banded vegetation patterning in Europe appear to have been carried out in Spain, where banded patterns in soils and vegetation form part of important discontinuities on semiarid slopes. Banding of the vegetation occurs at a scale of meters and is present in a scattered way along the contour lines. It consists of small discontinuous bands of vegetation located at the outer rims of small stony terracettes, behind which mostly bare and often crusted surfaces are found (Bergkamp, Cerdà, and Imeson 1999). In this environment, there is movement of surface water and nutrients from the less well-vegetated bands into the vegetation bands. Cammeraat and Imeson (1999) presented examples from two locations in southeastern and northeastern Spain where patterned or banded vegetation are found on seminatural and abandoned land or where vegetation is recovering from wildfire.

Runoff and Erosion Processes

Most studies have been concerned with runoff processes as such, with very few including erosion. The studies of runoff processes in different continents are first outlined, followed by erosion studies.

Australian Studies of Runoff

In Australia, the hydrological functioning of banded vegetation patterning has only been investigated at a few specific sites (Winkworth 1970). Earlier studies all concentrated on mulga woodlands. For example, Slatyer (1961) measured infiltration rates in the bands and interbands at Alice Springs by using 300-mm-diameter infiltration rings. The banding mainly consisted of the broad band pattern described by Mabbutt and Fanning (1987). The rates varied from 25 mm h^{-1} near the base of mulga trees to 10 mm h^{-1} in the interband areas. The work near Alice Springs also established that runoff occurred with rainfall events in excess of 10 to 15 mm and that it varied between 15% and 50% of rainfall depending on the intensity and duration of the event. It is probable that in the majority of rainfall events, the interband and the band constitute a closed system, with no net runoff through the tier. Perry (1970), working in the mulga woodlands near Alice Springs, concluded that for rainfall events up to 25-mm runoff was contained in the interband–band system. Mabbut and Fanning (1987) also carried out infiltration measurements in the Wiluna-Meekatharra study site at one narrow banding and one broad banding site. These results also showed that generally there were higher infiltration rates in the bands than in the interbands.

Recently, there have been several studies in semiarid and arid areas of Australia of the hydrological functioning of banded vegetation patterning with special emphasis on the soil surface conditions and plant properties that are responsible for both runoff generation and water harvesting processes (Greene, Kinnell, and Wood 1994; Dunkerley and Brown 1995; Dunkerley and Brown 1999). These studies have taken place in the semiarid mulga woodlands of eastern Australia, near Louth, New South Wales, and the arid chenopod shrublands in western New South Wales, near Broken Hill (see Figure 4.1). Each of these studies is now discussed in detail.

Louth (Lake Mere) Site, New South Wales (Mulga Woodlands)

The aim of the studies near Louth was to investigate the processes of infiltration and runoff in banded vegetation patterning and the effect of soil surface conditions on those processes. The Louth site was on Lake Mere station, 35 km north of Louth, New South Wales (see Figure 4.1), and consisted of an area of semiarid mulga woodlands having a banded vegetation pattern in near-pristine condition. The area has been extensively surveyed (Tongway and Ludwig 1990; Ludwig and Tongway 1995), the mulga banding at the site and the occurrence of three distinct geomorphic zones (Figure 4.3) were described. A range of techniques that measured soil hydraulic properties at different scales was then used in each of these three geomorphic zones (Greene 1992, 1993; Greene and Sawtell 1992; Greene, Kinnell, and Wood 1994).

The disc permeameter (Perroux and White 1988) was used to measure soil hydraulic properties at a potential of +10 mm (ponded) and −40 mm (nonponded). In the runoff and interception zones, the measurements were carried out on bare undisturbed surfaces away from the base of tussocks, and in the mulga bands, the A_0 layer of litter (mainly leaves from *Acacia aneura*) was carefully removed be-

Table 4.1. Disc Permeameter Measurements at Supply Potentials of +10 and −40 mm on Three Geomorphic Zones[a]

Final infiltration rates (mm h^{-1}) (supply potentials)[b]	Geomorphic zone			
	Runoff zone	Interception zone	Mulga band	Significance[c]
$\psi = +10$ mm	25.0	47.0	263.6	*
$\psi = -40$ mm	12.8	14.7	13.3	ns

[a] From Greene (1992).

[b] Quasi-steady-state outflow rate from the disc permeameter.

[c] * $p < 0.05$; ns, not significant.

fore carrying out the measurements. Under ponded infiltration (+10 mm), there were significant differences in the hydraulic properties between the three zones, as seen, for example, in the infiltration rates (Table 4.1). The mulga band zone has a significantly higher infiltration rate than the runoff and interception zones. However, at −40-mm supply potential, there were no significant differences in the infiltration rates between the three zones. These results can be largely explained by the presence of macropores in the mulga bands, as discussed later.

The difference in soil hydraulic properties between the three zones was further investigated by using a rotating disc rainfall simulator that applied a uniform rainfall intensity of 30 mm h^{-1}. Runoff was collected in a 1-m^2 steel quadrat carefully located in the ground directly under the nozzle (Greene and Sawtell 1992). The simulator was used in each of the three zones over areas of ground that were largely devoid of vegetative cover. The results obtained were similar to those obtained by Tongway and Ludwig (1990) (i.e., the runoff zone had the greatest runoff rate [~27 mm h^{-1}; Figure 4.4], the interception zone had the next highest [~10 mm h^{-1}], and the bands virtually had no runoff [0 mm h^{-1}]). There was no evidence of runoff from the mulga band, even after 40 minutes, indicating that the infiltration rate was maintained at greater than 30 mm h^{-1}. The two sets of infiltration data obtained by using the disc permeameter and the rainfall simulator both demonstrated the lower infiltration capacity of the soils of the runoff zone compared with soils of the interception zone and mulga band (i.e., runoff zone < interception zone << mulga zone).

Even though the rainfall simulator can be used to study the effects of surface crusting processes and vegetative cover on runoff generation, it is desirable to be able to relate these findings to what occurs during an actual rainfall event. Greene (1993) used large, completely bounded, runoff plots to measure the hydraulic properties of various units at Lake Mere. The plots, 5 m wide and 17 m long, were installed at right angles to the contours. At the bottom of the plot, overland runoff water was collected in a trough and led into a calibrated tipping bucket (Williams and Bonell 1988). Events were monitored by a Compulog data logger via a magnet attached to the bucket and a mercoid switch secured to the tipping frame. A tipping bucket rain gauge adjacent to the plots was also logged to provide rainfall data over time.

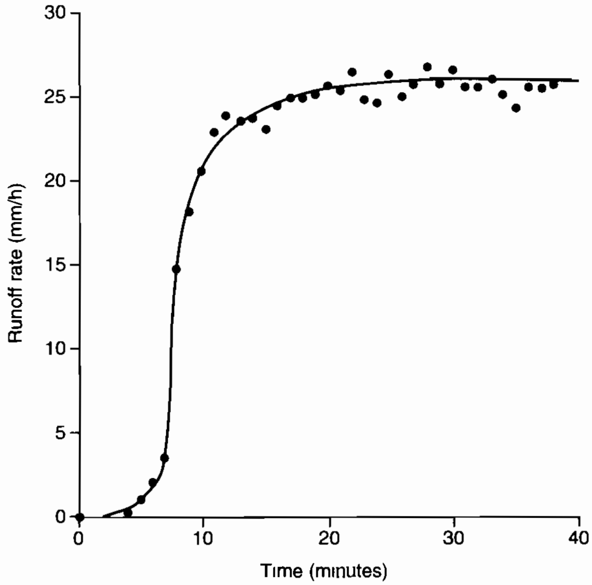

Figure 4.4. Infiltration behavior on a runoff slope.

Data from a typical rainstorm occurring on May 20, 1991, shows cumulative rainfall and cumulative runoff as a function of time (Figure 4.5), and assuming steady-state conditions exist, the difference between the two gives cumulative infiltration. During the first 18 minutes of this rainfall event, the averaged measured intensity of 22 mm h^{-1} was similar to that used in the rainfall simulator/cover experiments (i.e., 30 mm h^{-1}). It is interesting to note that the infiltration rates measured by using both methods were similar (i.e., 7.3 mm h^{-1} for the runoff plots compared with 11.2 mm h^{-1} for the rainfall simulator). Greene (1993) concluded that in some cases the simulator could be used to approximate very closely the infiltration and runoff conditions that occur during natural rainstorms. It is also interesting to note that during this event of 11.6 mm, the runoff coefficient Cr (volume of total runoff/volume of total rainfall) was 0.55, indicating that more than half the rainfall was lost as runoff. This is in agreement with the work of Slatyer (1961) and others (e.g., Winkworth 1970), who concluded that runoff from the interbands occurs with rainfalls in excess of 10 to 15 mm.

Runoff is shed to the bands downslope, where microrelief, vegetation, soil fabric, and surface litter cause the runoff to infiltrate. The redistribution of rainfall as runoff results in the interception zone and band receiving a larger proportion of the rainfall. Measurement of soil water contents after an event of 37.5 mm in March 1 to 2, 1987 indicated that the runoff zone, interception zone, and mulga band received 15.7, 33.7, and 51.6 mm of water, respectively (Greene 1992). The implications for herbage production as a consequence of the enhanced water status of

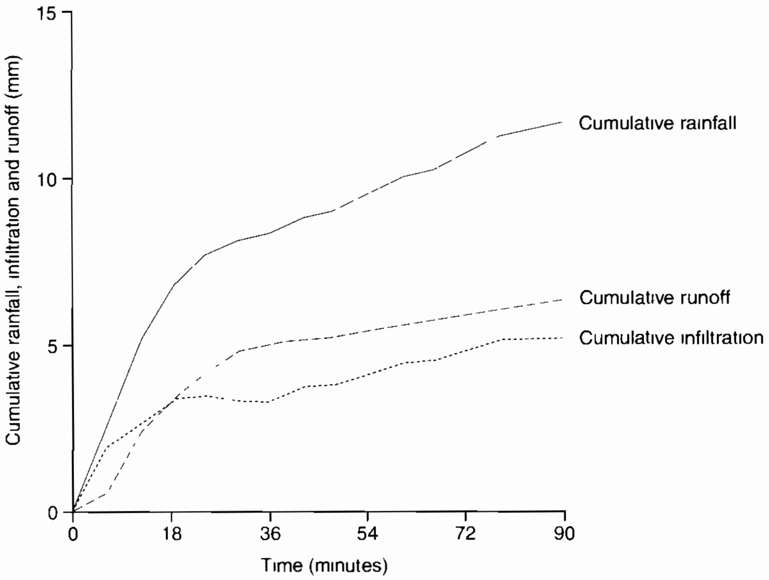

Figure 4.5. Cumulative rainfall, cumulative runoff, and cumulative infiltration on the runoff zone expressed as a function of time for a typical winter rainfall rainstorm.

the runon areas are discussed by Noble, Greene, and Müller (1998) and in chapter 11 of this volume.

Broken Hill Site, New South Wales (Chenopod Shrublands)

Dunkerley and Brown (1995) studied runoff and runon processes in patterned chenopod shrubland at a site near Fowlers Gap, 115 km north of Broken Hill (see Figure 4.1). The vegetation occurs on hillslopes having gradients of as little as 1% and displays a stepped microrelief of about 10 cm. Dunkerley and Brown (1995) observed that the bare surfaces shed surface runoff from rainstorms of as little as 4 to 5 mm and are thus a efficient source of runoff. Water accumulated on the lower margins of the bare zones where the gradient is lowest and then trickled into the vegetated areas, where it drained down abundant gilgai depressions (collapse features caused by a marked swell/shrink soil characteristic on wetting and drying).

Dunkerley and Brown (1999) further studied the effects of surface soil properties on hydrological behavior at another site approximately 40 km southeast of Broken Hill in a mixed chenopod shrubland-grassland community. They observed that surface roughness increases downslope through the interband and the zone of forbs at the upslope margin of a vegetated band, reaching its maximum within the vegetated band. Surface runoff is increasingly hindered during flow from the interband into the band by surface roughness. At the same time, soil resistance to entrainment increases in opposition to the shear forces generated by the runoff. In concert, these tendencies imply that little sediment transport is possible across the mosaic (Dunkerley and Brown 1999).

Macdonald, Melville, and White (1999) also described the interrelationships between soil cations, soil properties, and plant spatial variation in patterned ground at the Fowlers Gap site. The disc permeameter (Perroux and White 1988) was used in the patterned ground gilgai complex to detect differences in behavior between the bare areas and the vegetation bands. The microtopography of the patterned ground is generated by the gilgais (Mabbutt 1973). Macdonald, Melville, and White (1999) showed that the distribution of cations was not even. The cations, of which sodium is dominant, are concentrated within the bare areas. The sodium concentration decreases toward the center of the vegetation bands. The pattern of salt distribution was caused by the interaction of the preferential infiltration of water into the vegetation bands, the gilgai complex, and the vegetation-induced salt turnover. These factors cause the lateral movement of salts out of the vegetation bands into the bare ground.

Studies of Runoff in Other Continents

Africa

Banizoumbou Site, Niger (Tiger Bush). Several studies of the processes of runoff and erosion in banded vegetation patterning in Africa have been carried out. A major study of runoff production in a tiger bush catchment was carried out by ORSTOM (Peugeot et al. 1997) at a site located about 70 km east from Niamey in the west of Niger (Figure 4.6). The landscape is composed of dissected laterite-capped plateaus, with steep edge slopes that dominate wide topographic depressions located about 30 m below. The experimental site was located on a catena containing three main geomorphological units: (1) the plateau with loamy-clayey soils (30% clay) and low slope (0 to 0.5%), (2) the breakaway at the edge of the plateau (slopes: 4 to 8%), and (3) a dendritic drainage line at the break of slope. The plateau exhibits an alternating pattern of bare surface areas and vegetation bands roughly running along the contour lines (Ambouta 1984; Thiéry, d'Herbès, and Valentin 1995).

Precipitation exhibits an irregular distribution, but large storms occur from early May to late September, providing 95% of the annual rainfall, while the seven other months are dry. The mean annual rainfall for that region is 560 mm, calculated from 1905 to 1989. The storms are mostly convective. In this region, the median rainfall intensity is 35 mm h^{-1}, and 35% of the rain falls with an intensity greater than 50 mm h^{-1} (Lebel et al. 1992). Discharges from the catchment were measured from a gauging station located in the dendritic drainage line (Figure 4.6) and compared with that of a runoff plot located on the plateau bare soil surface (Table 4.2).

The results indicated that the runoff response to rainfall is quick, and there is no base flow. Base flow may occur in some drainage basins as a background flow component (Goudie 1990). Hortonian overland flow is the main process of runoff

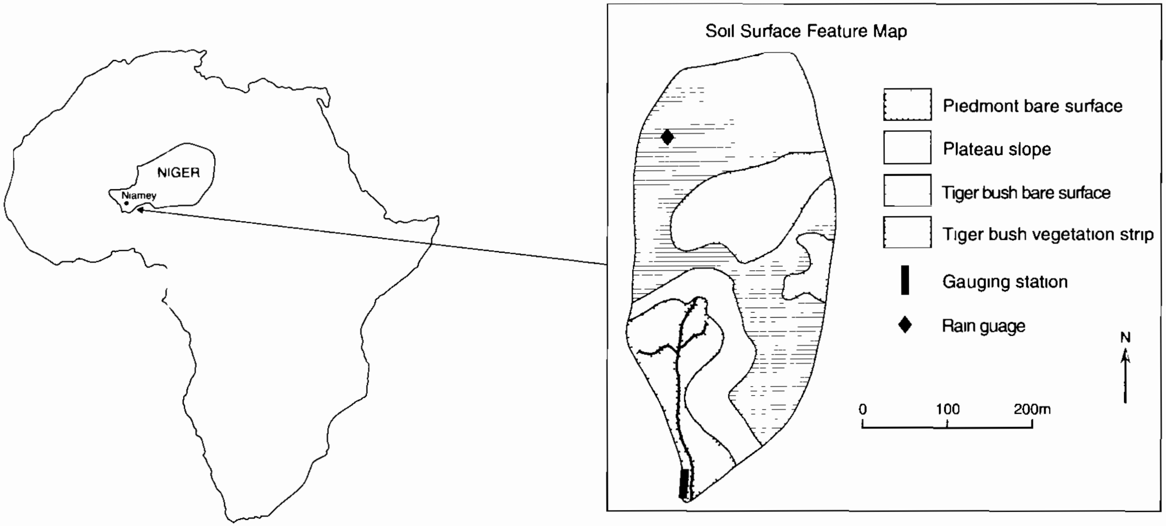

Figure 4.6. Location map of study site in Niger and soil surface feature map in catchment.

production in this region. Hortonian overland flow occurs during rainstorms after the soil's infiltration rate falls below that of the intensity of the rainfall. For the catchment, the mean seasonal values of the runoff coefficient Cr (volume of total runoff/volume of total rainfall over a season) observed during the two rainy seasons 1993 and 1994 ranged from 30 to 44% (Table 4.2), characterizing a catchment with high runoff production capability. At the runnoff plot scale, the values are slightly higher, ranging from 45 to 47%. Even though the number of floods is rather similar for the two observed years, the efficiency of the catchment was greatly increased in 1994. This difference between the 2 years does not appear at the runoff plot scale. The maximum Cr values were recorded for the storm on the July 21, 1994, which occurred under wet soil conditions. This storm produced similar values for the plot and the catchment.

The values of the runoff coefficient observed during the two rainy seasons allows the runoff capability of the catchment to be compared with that of a runoff plot located on the plateau bare soil surface (Table 4.2). The data collected in 1993 revealed that there are significant losses as the runoff moves from the zone of production to the catchment outlet. Both intermediate absorption and channel seepage on the plateau slope contribute to the decrease in flow. The overland flow produced on the bare surfaces runs into and is slowed down by the vegetation bands located perpendicular to the slope, and a significant part of the water infiltrates when crossing the vegetation bands. This explains the lower number of floods observed at catchment outlet, as the small storms do not produce enough runoff to reach the gauging station.

The difference in the mean runoff coefficient observed at the catchment scale between 1993 and 1994 is not observed at the runoff plot scale. The values of the runoff coefficient mean and maximum are very close at both scales in 1994. This was not the case in 1993. These differences can be explained by the greater amount of rainfall in 1994 (671 mm) compared with 1993 (484 mm) and its regular distribution during the second half of the rainy season that decreased the intermediate losses. The greater amount of runoff observed in 1994 was not the consequence of an increase in the runoff efficiency of the catchment but was due to lower surface water transfer losses. The soil moisture investigations made during the experiment are presented by Galle, Ehrmann, and Peugeot (1999) and chapter 5 of this volume.

Table 4.2. Runoff Coefficient Observed on the Catchment and on the Runoff Plot Situated on the Bare Zone of the Plateau

	Catchment 1993	Catchment 1994	Runoff plot 1993	Runoff plot 1994
Date	07/30 08/13	07/21	07/29	07/21
Number of floods	21	25	27	29
Runoff coefficient mean	30.3	44.1	45	47
Runoff coefficient max	44.7	68.7	71	69

Europe

A rainfall simulator was used in banded formations in three areas of Spain to quantify the surface water redistribution at fine spatial scales (Bergkamp, Cerdà, and Imeson 1999). These results were combined with an analysis of the rainfall magnitude-frequency characteristics of the three areas. There was a high variability in surface water redistribution, with most of the surface water originating from short storms of 10 minutes, duration.

North America

Cornet, Delhoume, and Montaña (1988) estimated that due to rainfall redistribution the vegetation bands in the Chihuahuan Desert in Mexico receive 1.5 to 2.5 times the rainfall at the site. Delhoume (1996) also describes that at his experimental site there are two scales at which water harvesting can occur. Although the vegetation bands of tiger bush function as previously explained, with runoff from the interbands into the runon zones, the overall tiger bush landscape is located in a runon zone at the foot of a long and crusted hillslope (Delhoume 1996). This type of two scale functioning has been also observed in areas of banded vegetation in Australia (J. Mabbutt, pers. comm.).

Studies of Water and Wind Erosion

As the artificial radionuclide cesium 137 (^{137}Cs) is an artefact of atmospheric nuclear weapons testing in the 1950s and 1960s, it can be used to measure erosion or deposition since then. Chappell and associates (1999) used this technique to measure erosion and deposition processes in Nigerien tiger bush. A 70-m transect encompassing two vegetation bands and the intervening bare band was studied. Using this technique, they showed that the net soil flux did not exceed the average annual dust accumulation rate (4 t ha^{-1} yr^{-1}) (Chappell 1995), although it did exceed the monitored 8-year dust deposition rate (2 t ha^{-1} yr^{-1}) for the region (Drees, Manu, and Wilding 1993). The discrepancy between these rates could be attributed to the imprecision of short-term monitoring and also to the difference in the efficiency of natural (vegetation) and artificial dust traps. These results suggest that the net soil gain at the depositional site was probably not only due to the accumulation of dust but also to some accumulation of material redistributed by surface wash. Single ^{137}Cs measurements from other vegetated bands and interbands in the region (Chappell 1995) have resulted in a net soil gain of 4 t ha^{-1} yr^{-1} and net soil loss of -3 t ha^{-1} yr^{-1}, respectively. These patterns correspond with the location of the erosion and sedimentation crusts identified by using a standardized classification (Valentin and Bresson 1992). Miles (1993) also used the radioactive isotope ^{137}Cs to measure soil erosion in the semiarid mulga woodlands on southwestern Queensland. Based on the ^{137}Cs profiles, the mulga lands of southwestern Queensland have lost approximately 30 mm of soil on average in the past 35 years. Besides water erosion, two types of semiarid, wind-induced vegetation patterning have been cited in the literature. One is related to former and leveled dunes, as described for northern Nigeria (Zonneveld 1999). Clayton (1966, 1969) referred to the same Sangwina sands. The orientation of the bands (about NNW to SSE) is perpendicular to the prevailing wind direction (ENE to WSW) during the period of formation of the former dunes. The other corresponds to present processes. In Mali, Leprun (1999) mentioned that on the bare crusted band, the eroded and sorted soil particles experience two different processes. The finer clay and loam fractions are removed downslope by the overland flow and accumulate in the depressions to form the wooded band where vegetation and fauna subsequently concentrate. The sandy particles are shifted by aeolian deflation and are deposited upslope, forming a microdune. In particular, the stratification, with a monoclinal lithology oriented NE to SW, namely, perpendicularly to the dominant wind direction and its slope facing the wind, controls the process and the direction of the band migration. Not being necessary to the formation of the contracted bush, the action of the wind would favor relatively rapid migration of the vegetation (up to 0.7 m yr^{-1}).

Effect of Soil Surface Conditions on Runoff

The runoff and erosion properties of banded vegetation are largely controlled by the nature of the soil surface conditions in the band and in the bare interband areas. Several factors influencing surface soil conditions in these two areas are discussed.

Macropores Resulting from Activities of Soil Biota

The results from the disc permeameter studies (Greene 1992) show the importance of pores greater than 0.75-mm diameter in conducting water into the soil. At a supply potential of –40 mm, when pores greater than 0.75-mm diameter are not contributing to water flow, the soils in each zone have similar infiltration rates (Table 4.1). However, the greatly enhanced infiltration rates (under ponded conditions) in the mulga band soils indicate that this sized pore must be prominent in these soils. These stable macropores of greater than 0.75-mm diameter, however, are largely absent from the upslope runoff areas. The absence of these pores in the runoff zones has been correlated with termite populations, which are lower in the interband areas compared with bands (Whitford, Ludwig, and Noble 1992). The differences can also be related to surface crusting (Greene 1992).

Surface Crusting

Surface crusting has been identified by many authors as the major factor of runoff production in the bare interbands. Difference in surface hydrology between the bare and the vegetated bands can be caused by variation in soil sealing due to a small difference in silt content between the two zones. Such differences have been ascribed to former early Holocene to late Pleistocene dunes leveled by sheet erosion (pediplanation) separated by filled-in valleys in northern Nigeria (Zonneveld

1999). Most often, the interband is subdividable in several parts characterized by surface conditions. Dunkerley and Brown (1999) noticed in Australia that the upslope part is relatively stone-free compared with the lower part. Thiéry, d'Herbés, and Valentin (1995) described the most common succession of surface crust along a transect across the bare interband. From a water-flow point of view, it is significant to consider the successive steps of the crusting process from the low fringe of the vegetated band to the destruction of the crusts within the core of the vegetated band.

In the downslope edge of the vegetated band, vegetation declines because of a chronically insufficient water supply. Owing also to the reduced litter cover and soil-faunal activity, structural crusts tend to develop. They consist of three well-sorted layers. The uppermost layer is composed of loose coarse sand; the middle one consists of fine, densely packed grains with vesicular pores; and the lower layer shows a higher content of fine particles with considerably reduced porosity. Frequently, the upper layer contains very fine gravel and very coarse sand. The well-defined textural differentiation results from a process resembling the particle size discrimination obtained from a nest of sieves, hence the term *sieving crust* is given to this type (Valentin and Bresson 1992). Raindrop impact forms microcraters, the walls of which present a clear vertical sorting of particles. Wind and runoff can readily remove loose particles in the sandy microlayers of the sieving structural crusts. The lower fine-textured layer is responsible for the low infiltration rates of such crusts (Casenave and Valentin 1992).

In the bare areas, three major types of crust occur in a more-or-less clear succession: erosion, pavement, and sedimentation crusts. Erosion crusts are built up with a single smooth hard layer made of fine particles. Porosity is restricted to a few cracks and vesicles, so that the infiltration rate is low. Erosion crusts are formed of sieving crusts from which the loose sandy layers have been removed by overland flow and wind. They mainly occur in the upslope part of the bare areas and develop a dark patina, most likely due to colonization by cyanobacteria (Malam Issa et al. 1999). Once formed, these crusts promote runoff and are usually not observed to be colonized by vegetation because of the impedance they provide to seedling emergence and the dry pedoclimate they produce. Wind and overland flow invariably remove seeds that may be deposited on the soil surface.

Pavement crusts contain coarse fragments embedded in a crust the microstructure of which is similar to the sieving crust described above. Vesicular porosity is much more pronounced, especially below the coarse fragments. The distribution of patches with pavement crust is rather indiscriminate due to the irregularity of the depth of the gravel layers. Because these pavement crusts tend to armor the soil underneath, they tend to protrude slightly from the adjoining erosion crusts. Such pavement crusts are also common in the bare interband of banding patterns in Australia (Dunkerley and Brown 1999; Macdonald, Melville, and White 1999).

Sedimentation crusts or "still depositional crusts" (Valentin and Bresson 1992) consist of densely packed and well-sorted particles, the size of which progressively increases with depth. The vertical particle-size distribution, with coarser particles at the bottom and finer particles at the top, is the reverse of that observed in the sieving crusts. When dry, these crusts often break up into curled-up plates. "Still-depositional" crusts form in standing water and develop where surface flow is hindered. In puddles, the larger particles sink rapidly and form the bottom layer, whereas the finer particles deposit at the top. During drying, cracks and curled plates can develop owing to the difference in shrinkage forces among the microlayers. These crusts develop in the lowest patches of the bare areas, directly adjoining the grassy depositional open bush areas.

The general distribution of the three major types of crust can be modified due to local topographic accidents, but it is common in many bare interbands of banding patterns, for example, in northern Mexico (Janeau, Mauchamp, and Tarin 1999). In the grassy areas that correspond to the upper zones of the vegetated bands, the crusts are depositional but differ slightly from those previously described. They are often more platey in structure, do not curl up, and are often colonized by algae ("microphytic sedimentation crusts" or "microbiotic crusts") (Eldridge and Greene 1994). Their pronounced porosity consists of numerous broad cracks (1 to 2 mm) and abundant holes perforated by termites. In the core of the vegetated bands, the thick litter provides an efficient protection to soil surfaces, but intense termite activity tends to destroy the crust (Ouédraogo 1997). However, this litter and the faunal activity are not uniform, so that in some patches the previous crust can be locally maintained.

Comparison of the infiltration rates of the crusts in the interband area demonstrated that the final infiltration rates measured with the rainfall simulator were lower than those measured with the disc permeameter. Therefore, the additional effects of raindrop impact and surface flow obtained with a rainfall simulator cause the soil to have a lower permeability. Greene and Ringrose-Voase (1994) further investigated the hydrological properties of surface crusts occurring on the runoff zone. The crusts examined were of two types: those that had been present for sometime, and those that were recently generated by using the mobile rainfall simulator. Micromorphological examination of the surface crusts distinguished four main categories of surfaces that were always present in a crust (i.e., a matric crust, skelic crust, porphyric crust, and disturbed crust). These categories were described according to Brewer and Sleeman (1988). The matric crusts have a concentration of clay at their surface as a thin crust of clay microaggregates approximately 50 μm thick, whereas the skelic crusts are 500–800 μm thick and consist of a concentration of sand-sized quartz grains at the surface. Porphyric crusts have no fraction concentrated at their surface, and a disturbed crust is broken up. Because the categories are based only on the immediate surface layer alone, it is not always possible to relate them to crust categories used by other workers. Nevertheless, the matric crust and skelic crust relate, respectively, to the erosion and sieved structural crusts described by Valentin and Bresson (1992).

Examination of the crusts showed that the proportions in the various categories change as the soil is subjected to different treatments. Therefore, it is probable that in the soil from the runoff zone, the crust morphology observed after a single significant rainfall event gradually reverts during a dry period to a condition similar to that found before the event. Greene and Ringrose-Voase (1994) proposed that the micromorphological properties of surface crusts are cyclic over time. Because the microstructure of surface crusts has a large effect on soil hydraulic properties, it is probable that the infiltration rate would also be cyclic over time, decreasing during rain and increasing progressively again after dry periods. This was shown by some additional infiltration measurements carried out with a disc permeameter on the runoff slopes. Greene and Ringrose-Voase (1994) showed that after a series of high-intensity rainfall events in 1988, the soil infiltration rate dropped from 24.0 to 5.1 mm h^{-1}. However, during the subsequent dry period the rate returned a similar value (23.0 mm h^{-1}) to the prerainfall event. Others researchers have also observed similar seasonally cyclic patterns in soil properties, for example, in grazed pastures in West Africa (Casenave and Valentin 1989) and in Texas in the United States (Thurow, Blackburn, and Taylor 1988).

Vegetative Cover

Besides surface crusting, the other major surface property affecting infiltration and redistribution of water on the runoff zones will be surface vegetative cover, particularly that of perennial grasses. Even though the vegetative cover in the runoff zone at Lake Mere is relatively low (i.e., 7% grass cover) compared with that in the interception zone and mulga band (Tongway and Ludwig 1990), the role of vegetative cover in this zone is still important. There are two main reasons for this: (1) the vegetative cover protects the soil surface from raindrop splash and surface sealing effects, and (2) there is a positive feedback from the vegetative growth into the soil in the form of maintenance of nutrients, especially organic carbon, which improve soil stability (Tongway and Ludwig 1994). Both of these effects would be expected to improve infiltration and water-holding capacity.

Rainfall simulations using a uniform intensity of rainfall (30 mm h^{-1}) were carried out on cover levels ranging from bare ground to approximately 80% total projected cover of perennial grasses (Greene, Kinnell, and Wood 1994). The cover levels were recorded by taking a photograph of the 1-m^2 quadrat by using a camera mounted 1.5 m directly above the plot. Cover included both dead and alive perennial grasses, as well as litter. The runoff measurements were carried out at a constant low stocking rate (0.2 sheep ha^{-1}) to avoid problems with possible direct effects of stock grazing on the soil surface and hence on hydrological properties. There was a highly significant negative relationship between the final runoff rate (y) and the amount of plant cover (x) (Figure 4.7):

$$y = 22.3 - 0.15\,x; \ (r^2 = 0.58;\ n = 15,\ p < .01)$$

The final runoff rates for a high stocking rate paddock (0.53 sheep ha^{-1}) are also shown in Figure 4.7. The average of these, 23.4 mm h^{-1}, is not significantly different from the average final runoff rate (22.3 mm h^{-1}) at 0% cover for the low stocking rate, indicating that in this experiment the two stocking regimes had not influenced runoff other than through their effect on cover.

Several other workers have already demonstrated in rangelands that vegetative cover leads to lower runoff and higher infiltration rates. For example, Scholte

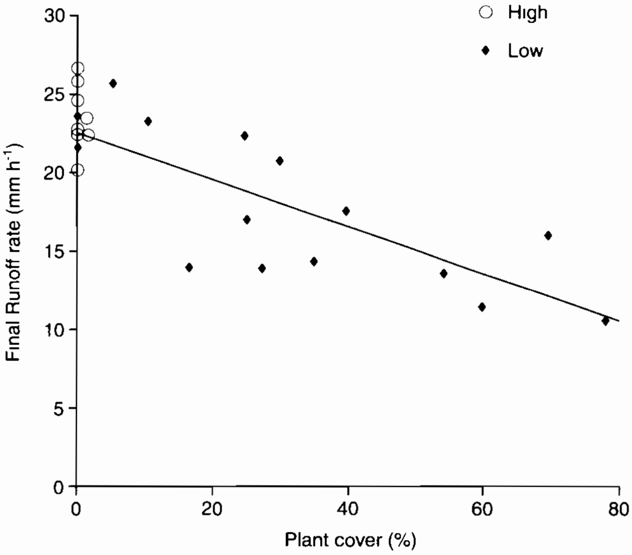

Figure 4.7. Effect of plant cover on final runoff rate.

(1989) showed that there was a greater infiltration rate under shrubs than on the sealed surface soil. Lyford and Qashu (1969) and Blackburn (1975) showed that the infiltration measured near the stems of plants was higher than the area between plants.

Compressive Stress and Bulk Density

Soil susceptibility to water erosion is usually related to compressive stress and bulk density. These characteristics have been assessed along two banded vegetation transects in Australia by Dunkerley and Brown (1999). Unconfined compressive strength (UCS) of the uppermost 1 to 3 cm of regolith was measured at 1-m intervals along the transects with a hand-operated penetrometer equipped with interchangeable domed tips. The patterns of UCS were not entirely regular. However, profiles at both sites display values that generally remain less than 500 kPa. The prominent peaks (2,000 to 3,000 kPa) are associated with zones of forbs (defined as herbaceous nongrass species occurring in savanna grasslands) (Goudie 1990). These zones may coincide with greater amounts of cementing agents such as carbonates or clays delivered from upslope. The trends support the notion that increasing deposition of binding agents of some kind within lower microtopographic elements has occurred. Prominent peak of bulk density (1.48 g cc^{-1}) was recorded at or near the zone of forbs. Within the bands, bulk density fluctuates irregularly (1.33 to 1.41 g cc^{-1}) and tends to be lower than in interbands (1.37 to 1.39 g cc^{-1}). The data are consistent with more frequent dilations of soils within the bands and with their more abundant organic matter, and hence with a more porous, open, and friable soil structure.

Management of Runoff and Erosion in Banded Vegetation

From the previous sections, it can be seen that banded vegetation systems are self-generating and provide a natural water harvesting situation. Valentin and d'Herbès (1999) developed a simple model of rainwater redistribution based on a crust typology relating surface characteristics to hydrological properties (Casenave and Valentin 1992). They found that the ratio between the watershedding zone (which includes the lower decaying part of the vegetated band) and the infiltration zone (restricted to the core of the vegetated band), based on field crust survey, was a better predictor for the water harvesting efficiency of the system than was the interband–band ratio. This water harvesting model could be used as a satisfactory predictor for woody biomass. These authors showed that the water harvesting and concentration process enables wood production equaling that of the forest in much more humid southern zones. The woody biomass of unpatterned vegetation remains approximately half of that of the tiger bush.

Erosion processes can also assist in maintaining the structure of banded vegetation. The erosion processes operating in the banded vegetation act to establish and maintain a series of erosion cell mosaics. Taken together, the topographic sequence of bare interbands and vegetated bands (or in the case of mulga woodlands, three zones: runoff zone, interception zone, and mulga band) make up a single unit referred to as an erosion cell (Pickup 1985). During high-intensity rainfall events, the interband (or runoff zone) sheds water, sediment, and nutrients to the vegetation band (or interception zone and the mulga band). Under a stable system, the losses from the runoff zone (production zone) are balanced by the gains in the mulga band (deposition zone).

The key management question is how do we manage this banded vegetation patterning to ensure the maintenance of the processes of water redistribution and that water is not lost out of the system? This is discussed in detail in chapter 11 of this volume. There are many recorded instances in which poor management has been attributed with effects detrimental to this aim. For example, Mabbutt and Fanning (1987) discussed how degradation of banded vegetation patterning in the Wiluna-Meekatharra area of Western Australia occurred as a result of overgrazing. They reported that moderately degraded mulga woodlands in the Wiluna-Meekatharra area of Western Australia were characterized by bare sheet-eroded interbands and gullying to hardpan on the lower margins of the bands. Greene, Kinnell, and Wood (1994) also discussed the implications of overgrazing on the functioning of the mulga band in the semiarid rangelands of eastern Australia. Overgrazing not only increased the amount of runoff into the bands, but their high infiltration rates were also lowered. Under heavy rainfall events, excess runoff would bypass the bands and be lost out of the land system. The end result is the breakdown of the banded vegetation patterning. Dunkerley and Brown (1995) also showed that similar degradation can occur in arid chenopod shrublands. Tongway and Ludwig (1997) described such landscapes as dysfunctional. Valentin, d'Herbès, and Poesen (1999) further discussed the role of both human disturbance and climate change in altering banded landscapes.

The key tactical approach is to set management-induced impacts to maintain current infiltration rates in the interbands (thereby not greatly increasing the current amount of runoff) and to maintain the infiltration capacity of the bands such that the system behaves as a closed tier (Greene, Kinnell, and Wood 1994). In addition to grazing, road construction, drainage works, and pasture improvement, all need to be managed to maintain the hydrology of the patterned surfaces. The processes of runoff and redistribution are thus critical for maintaining a highly efficient system of water harvesting and primary production in systems of banded vegetation patterning in both arid and semiarid environments.

Summary

We have outlined the results of various soil runoff and erosion studies in a range of continents. They have all demonstrated the role of rainfall infiltration and redistribution as essential characteristics for the maintenance of banded vegetation patterning. The marked differences in soil hydraulic properties between the two mosaic phases (i.e., higher infiltration rates in the bands compared with the interband areas) largely account for the redistribution of water that occurs during rainstorms. The differences are largely controlled by the surface soil conditions of the respective zones, particularly the high crusting tendency of the interband surface, coupled with the high amounts of perennial grass and shrub cover in the vegetative band. The redistribution of water and its concentration in the runon areas further enhances the levels of cover in the vegetation bands, which, in turn, enhances soil physical properties, especially infiltration rates.

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5. Soil Water Balance

Sylvie Galle, Joost Brouwer, and Jean-Pierre Delhoume

Introduction

In the more than 80 references related to banded vegetation patterns, five continents and 12 countries are represented. The early research concerned only the vegetation pattern itself (Clos-Arceduc 1956). Hypotheses regarding ecological functioning were then proposed between 1956 and 1970 and clearly synthesized by White (1971) for seven countries. He defined the minimum common characteristics necessary for the existence of banded vegetation spatial structure. These characteristics are now well known and include a semiarid climate, high-intensity rainfall, and a gentle slope. These characteristics are cited in almost all the publications on banded vegetation. We will not further review them here but focus instead on what they imply: the importance the spatial redistribution of water in the dynamics and the functioning of tiger bush bands. The areas of sealed, substantially bare soils yield a high proportion of runoff. On encountering the thicket bands immediately downslope, the flow rate diminishes and infiltration occurs, thus providing an additional water supply to the thicket. This process is more active in the upslope part of the thicket and progressively decreases to nil on the downslope edge, where many dead trees are observed. The zone located immediately upslope of the thicket is often called the "pioneer front" (Table 5.1) and is a zone of active plant colonization. Recently, a mathematical model based on two hypothesis: (1) competition for water resources along the slope and (2) synergy with lateral neighbors was successful in reproducing a banded structure from an initially random dis-

Table 5.1. Names Used by the Various Authors to Refer to the Functional Zones Forming a Banded Vegetation Unit

	Australia patterned mulga woodland		Mexico two-phase mosaic "mogote"	Niger tiger bush	
Functional zone	Alice Springs	Lake Mere	Mapimi	Banizoumbou	Say
Bare/herbaceous areas					
Upslope bare area			Downhill bare area		
Central bare area	Intergrove	Runoff zone	Bare area (transit zone)	Bare soil	Bare area
Downslope bare area (pioneer zone)		Interception zone	Deposition area (pioneer zone)	Upslope border (pioneer zone)	Grassy open bush
Bushy areas					
Upslope grove			Upslope vegetation (screen of *F. cernua*)		
Central grove	Grove	Mulga grove	Dense bushy area	Thicket core	Closed bush
Downslope grove			Rear edge of dense bush	Downslope border (senescence zone)	Bare open bush

tribution of vegetation (Thiéry, d'Herbès, and Valentin 1995; Dunkerley 1997). The outputs of these modeling exercises underline the overriding influence that differential spatial water availability has on the formation of vegetation bands.

Despite the obvious importance of water redistribution in tiger bush functioning, only a few studies have actually tried to confirm and quantify the processes and outcomes. In this chapter, we review and compare those studies, which are concerned with quantification of soil moisture, runoff, and evapotranspiration patterns at banded vegetation sites. The studies cover three countries, Australia, Mexico, and Niger, located on three continents. We compare the main results obtained and discuss the similarities as well as the differences between the sites.

One issue that can complicate such a comparison is a difference in terminology. Table 5.1 summarizes the names used for various zones in banded vegetation areas in each continent. In a banded vegetation unit, up to six functional zones can be recognized. These zones can be grouped more generally into "bare area" (including bare soil and sparse annual herbaceous cover) and "vegetated area" (composed of shrubs and/or trees). The precise terminology and definitions of the various functional zones are included in the description of each site.

Australia

The arid and semiarid mulga lands of Australia, where mulga (*Acacia aneura* F. Muell.) forms a significant part of the vegetation, comprise an estimated 1.5 million km^2. These mulga lands can exhibit a banded vegetation pattern (Figures 1.12, 1.13a,b, this volume; chapter 1, this volume). Such a pattern has most commonly been reported from woodlands growing on gentle topographic gradients, where wooded bands are essentially parallel to the contour, separated by sparsely grassed treeless areas. *Acacia aneura* banding has been described as "band–interband" patterning in Western Australia (Mabbutt and Fanning 1987), central Australia (Slatyer 1961), and eastern Australia (Tongway and Ludwig 1990; Dunkerley and Brown 1995).

As Dunkerley and Brown (1995) mentioned in their critical bibliographic analysis of patterned chenopod shrubland in Australia, the literature on vegetation patterning contains a wealth of hypotheses but few firm data. This section deals with results of quantitative studies relating to the soil water balance of patterned vegetation areas in Australia. The presentation focuses on two sites near Alice Springs (Northern Territory) and at Lake Mere (New South Wales).

Alice Springs

Description

Slatyer (1961) investigated this site where classical examples of banded vegetation patterning were found: the area was semiarid (250-mm annual rainfall), with a single rainy season (75% of the rain falls during the 6 summer months) characterized by high-intensity rainstorms. The potential evapotranspiration was high compared with rainfall (2,410 mm yr^{-1}). In addition, the average slope was gentle (0.2%). The interbands had a slightly greater slope than the bands. At this site, individual trees of *A. aneura* (mulga woodland) occurred in bands 5 to 50 m wide and 20 to 400 m long. The interband areas were three to five times as wide as the bands. The soils were highly weathered and of low fertility and had crusted surfaces. There was a marked difference in soil permeability between the band and interband areas, and within the band, permeability was higher close to the trees. The experimental site occupied an area of 25 ha and included three complete band–interband units (Slatyer 1961).

Quantitative Results Related to Soil Water Balance

Although the degree of runoff varied with the amount and intensity of the rainfall, as well as with antecedent soil water, substantial runoff from the interband normally took place with rainfall in excess of 15 mm. With heavier rainfall events, infiltration after rain was almost twice as great in the bands as in the interbands. Given the average widths of the bands and interbands, this represented a runoff percentage of about 20% from the interbands. No deep drainage below 200 cm (access tube depth) was found for the 18 access tubes.

Within the band, Slatyer (1961) clearly underlined the importance of trees in creating a heterogeneous soil water distribution. First, part of the rain is intercepted by the foliage and channeled down the branches and trunks. When rainfall intensity was less than 25 mm h^{-1}, the amount of stem flow was approximately 40% of the rainfall expected on an area equivalent to the horizontal projection of the canopy. Second, the infiltration capacity of the soil was higher close to the trees. Marked differences were found in the infiltration rates measured with a positive pressure head. The infiltration rates varied by a factor of 2 between interband (10 mm h^{-1}) and band (22 mm h^{-1}), but also within the bands: from 22 mm h^{-1} at 0.5 m from tree trunk to 15 mm h^{-1} at 2 m from tree.

Slatyer (1961) investigated differences in evapotranspiration by measuring changes in the soil water content. This was possible because there was no deep drainage. The changes in soil water content (equal to the actual evapotranspiration [AET] were divided by the potential evapotranspiration [PET]) and then plotted against available soil water storage (Figure 5.1). Zero soil water storage was the minimum value measured after a summer period of about 3 dry months. It can be seen that the initial values of AET/PET were close to unity in the interband and were lowest (0.6) closest to the trunk, where most shade occurred. In the interband, after an initial rapid loss of water by direct evaporation from the moist surface horizon, there was a sudden drop in evapotranspiration, as the surface soil dried, to a value determined mostly by the transpiration component. Under the bands, these decreases were much more gradual, with no great difference between 0.5 and 2.0 m from the tree trunk. Slatyer (1961) combined these data with changes in soil water profile and concluded that in the band, most evaporation occurred within 2 to 4 days after rain; afterward, transpiration was the main cause of water loss.

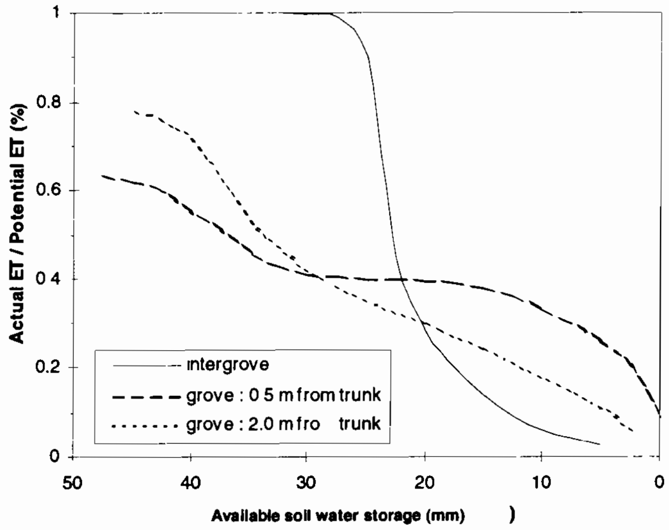

Figure 5.1. Soil water extraction in banded vegetation. Alice Springs (Australia). (Modified from Slatyer 1961.)

The main quantitative soil water balance information from the Alice Springs site is summarized in Table 5.2. From this information, it may be deduced how much extra water the vegetated areas received on average. We know that runoff represented 20% of rainfall events exceeding 15 mm; moreover, 80% of rainfall events are less than 12.5 mm (40% of the total rainfall). Significant runoff was observed for only a few events, typically four rain events of 25 to 33 mm yr^{-1} (or 100 to 132 mm). For these events, ponding and deep soil water penetration were observed in the bands. Thus, about 25 mm or 10% of annual rainfall ran off from the bare areas to the bands. However, as the interbands were three to five times as wide as bands, this translated to an average extra 75- to 125-mm water supply per year, in addition to the 250 mm that fell directly on the vegetated areas. Average annual infiltration in the band areas was thus approximately 140% of rainfall.

Lake Mere

Description

This site located in eastern semiarid Australia was first described by Tongway and Ludwig (1990). This pastoral production zone was selected for its good condition of the *Acacia aneura* vegetation, due to historically low grazing pressure. Average annual rainfall was 308 mm and characterized by large variability both within and between years. Unlike Alice Springs there was no marked rainy season; rain can fall at any time of the year. The overall slope of the site was less than 0.5%.

Table 5.2. Main Characteristics of Studied Sites Related to Soil Water Balance Quantitative Information

	Australia		Mexico	Niger (Africa)	
	Alice Springs	Lake Mere	Mapimi	Banizoumbou	Say
Annual rain (mm yr^{-1})	250	310	270	560	
Coefficient of variation (CV) of rainfall (%)			25	26	
Rainfall events distribution	80% (<12 mm)		80% (<10 mm)	60% (<10 mm)	
Slope (%)	0.2	<0.5	0.6	0.2	<1
Thicket width (m)	5–50		20–70	10–30	10–30
Concentration ratio bare/vegetated areas	3–5	1.3	3.5	2–3 2	
Soil difference bare/vegetated		No	No	No	Yes
Macroporosity in stripes		1 mm	Yes	Yes	6 mm
Runoff (% P) (threshold)					
Central bare	20% (>15mm)	55% (?)	100% (>4mm)	70% (>5 mm)	
Downslope bare				15% (>30 mm)	
Downslope grove				42% (>15 mm)	
Infiltration[a] (%P)					
number of studied events	?	1	16	60	4
Upslope bare	—	—	28%P	—	—
Central bare	80%P	40%P	22%P	20%P	22%P
Downslope bare	—	90%P	82%P	85%P	100–300%P

Upslope grove	—	—	152%P	—	—
Central grove	160%P	140%P	200%P	400%P	200%P
Downslope grove	—	—	123%P	40%P	<P
Annual infiltration[b] (%P)					
Author	Reinterpretation	—	Mauchamp et al. (1994)	Galle et al. (1999)	
Upslope bare	—	—		—	
Central bare	90%P		52%P	46%P	
Downslope bare	—			98%P	
Upslope grove	—	—	283%P	—	
Central grove	140%P		300%P	277%P	
Downslope grove	—	—	137%P	82%P	
Actual evapotranspiration[c]					
Bare			61%P		42%P
Grove			287%P		210%P
					Reinterpretation
Deep drainage	No	No	No	Yes	2–5%P

?, estimated values; —, no data available.

[a] Measured infiltration in the different zones during runoff events

[b] Modeled infiltration over the year (including low rainfall events)

[c] Modeled actual evapotranspiration for average year.

Between band and interband areas, Tongway and Ludwig (1990) described a "grass band" that they called an interception zone (see Table 5.1), associated with the upslope side of bands and occupying 12% of the site. Although noted, such grass bands were not described as an important component of the banded mulga lands of western and central Australia (cf., e.g., Slatyer 1961). Tongway and Ludwig (1990) suggested that this difference could simply be due to differences in livestock grazing pressure, although the Lake Mere site had higher and more reliable rainfall than the other sites reported from Australia. The mulga bands at Lake Mere had only 52% total vegetation cover (12% grass, 40% trees), whereas 20% grass cover was observed in the interception zone and 7% grass cover in the runoff zone. The runoff zone had a stony, strongly crusted surface soil, the interception zone had some cracks, and the runon zone of the mulga bands was covered with litter. Greene (1992) measured infiltration in the field by using a disc permeameter (200-mm diameter) at water supply potentials of –40 and +10 mm. He studied 12 line transects with three replicates in each of the zones.

Quantitative Results Related to Soil Water Balance

Under unsaturated conditions (–40-mm pressure head), there were no significant differences in the sorptivity and infiltration rates between the three zones (Table 5.3). But under saturated conditions (+10-mm pressure head), the soils in the mulga band had five to ten times higher infiltration rate than the soil in the runoff and interception zones (Table 5.3). At negative potential, only the soil matrix was active in conducting water into the profile, and as the soil was of similar textural composition under band and interband, no significant difference was observed in infiltration rate. Under ponding conditions, the presence of macropores allowed rapid infiltration. A positive 10-mm water potential allowed macropores of greater than 0.75-mm diameter to conduct water. Stable macropores (1-mm-diameter pores) were due to faunal activity (ants and termites), plant roots, or cracks were observed in the mulga band and, to a lesser extent, in the interception zone soils but are absent in interband.

Table 5.3. Disc Permeameter Measurements (200-mm diameter) at Supply Potential of +10 and –40 mm on the Three Geomorphic Zones in Lake Mere (Australia)[a,b]

	Supply potential of +10 mm			Supply potential of –40 mm		
	Runoff zone	Interception zone	Mulga grove	Runoff zone	Interception zone	Mulga grove
Sorptivity (mm h–1/2)	13.1	20.5	22.7	16.2	16.6	17.0
Hydraulic conductivity (mm h^{-1})	20	32	245[c]	6	8	6

[a] Each measurement is a mean of 36 replicates

[b] From Greene (1992).

[c] Significant difference between means $p =$ 05.

This difference in hydraulic properties resulted in a major redistribution of water between the three zones. After a rain event of 37.5 mm, 16 mm (42%) infiltrated in the runoff zone, 34 mm (90%) in the interception zone, and 52 mm (138%) in the mulga band. Even though water from the runoff zone passed across the interception zone, infiltration there was still less than 100% of the incident rainfall.

The difference in soil physical properties between the three zones were due to a combination of geomorphic processes and the amount of vegetation cover in the different zones. Vegetation had a positive feedback in terms of maintenance of a nutrient cycle and protecting the soil surface from raindrop splash, thus preventing surface sealing. Bioturbation of the soil by fauna such as ants and termites involved in organic matter cycling provides stable biopores for water transport (Tongway, Ludwig, and Whitford 1989). All these factors resulted in the soil under vegetation having improved physical properties such as structural stability and infiltration rate.

The infiltration rates obtained with the disc permeameter on interband areas were later compared with rainfall simulator and runoff plot data (Greene 1993). Infiltration rates for the interband measured by using a rainfall simulator (11 ± 2 mm h^{-1}) were similar to those measured by using a runoff plot during a natural rainfall event of similar intensity (and to those measured with a ring infiltrometer at Alice Springs by Slatyer [1961]). The soil types at Alice Springs and Lake Mere are similar. The infiltration rates measured with the disc permeameter had a higher mean and a wider range (20 ± 12 mm h^{-1}). This is probably due to the smaller area sampled by the permeameter and underlines the spatial variability of infiltration even at fine scale. Although lower than between zones, the intrazone variability of infiltration rate was significant.

Analytical Model

Based in part on the results from Lake Mere, the water and vegetation dynamics of semiarid landscapes were analyzed by Ludwig, Tongway, and Marsden (1994). They proposed a flow- filter model based on the hypothesis of Noy-Meir (1973): given resource limitations, the concentration of natural resources from source areas into sinks result in a level of landscape productivity that is higher per unit area than if resources are uniformly dispersed over the landscape. The vegetation patches act as sinks by filtering and concentrating water and nutrients lost from source areas (i.e., interbands). The aim of the flow-filter model was to determine the area of sink needed to conserve all water within a landscape. In the model, runoff is a function of rainfall input, soil infiltration rate, soil water storage capacity, slope, fetch length, and landscape area. Thus, both the level of water input and the filtering capacity and width of a sink will affect whether any water is lost from the system to the next sink or out of the landscape system.

The simulation model was run using topographic soil and vegetation parameters derived from a range of studies at Lake Mere. They found that for a low rainfall year (160 mm), no water ran out of the bands until they decline to 40 to 60% of the total surface. This closely matched the total area of landscape sinks observed

(43%). However, with 320 mm of annual rain, typical for the site, the system will lose water, even for a completely covered surface. This emphasizes the fact that, although vegetation of semiarid areas has to face high spatial and temporal variability of rain, the system is optimized to survive drought conditions.

Mexico

A two-phase mosaic scrubland, or banded vegetation patterning, in northern Mexico was first described by Cornet, Delhoume, and Montaña (1987). These formations are located in the Mapimi Biosphere Reserve, which forms part of the Chihuahuan Desert (Schmidt 1979). The hydrological functioning of these vegetation formations was investigated experimentally over a 4-year period. The results of these studies are summarized here.

Mapimi

Description

A representative toposequence of the Mapimi Biosphere Reserve was studied that included areas of two-phase mosaic scrubland (Delhoume 1988). The landscape toposequence was 10 km long. It started at a small ridge (cerro) with a maximum height of 1475 m and pronounced slopes (>20%). The elevation and slope decreased over the "bajada" (5% to <1% slope) and finally to the "playa" (slope of <1%). The two-phase mosaics were commonly situated on the gentle slopes of the lower "bajada" (~0.5%). They represented 32% of the 172,000 ha of the Mapimi Biosphere Reserve (Montaña 1992).

The climate was classified as an "arid tropical, continental climate, at medium altitude, with summer rains and cool winters" (Cornet, Delhoume, and Montaña 1988). The average annual potential evapotranspiration calculated by the Penman method was 1800 mm. The average annual rainfall was 279 mm, with a coefficient of variation (CV) of 25% (1978 to 1992). About 70% of rain fell in the 4 months from June to September. Storms were torrential but did not last long: 99% of rainfall events were less than 40 mm and 80% less than 10 mm, representing, respectively, 92% and 37% of total annual precipitation. The rainfall was characterized by strong variability both spatially and temporally (Delhoume 1996).

From a hydrological point of view, the zone formed part of one of the closed (endoreic) basins of the Chihuahuan Desert. The surface runoff occurred as dispersed sheet-flow where the slope was less than 2% and was more concentrated in unchanneled shallow linear depressions or water lanes where the slope exceeds 2% (Breimer 1988).

In aerial photographs (Figure 1.10, this volume), the Mapimi tiger bush appears as a mosaic of dense vegetation bands (or vegetation arcs), alternating with barren zones (Cornet, Delhoume, and Montaña 1988; Cornet et al. 1992). The main axis of every band follows a contour line: lengths of band range from 100 to 300 m and widths from 20 to 70 m. Bare zones were three to four times as wide as the vegetated bands.

Mosaic units at Mapimi were divided into five zones by Cornet, Delhoume, and Montaña (1987). From upslope to downslope, they distinguished (upper part of Figure 5.2)

1. a transit zone with bare ground: the soil surface was covered by erosion and pavement crusts indicating high runoff potential (K_r = 80 to 90% (Casenave and Valentin 1992)
2. a deposition area or pioneer zone covered by sedimentation crusts with polygonal cracks; this pioneer zone was colonized by a sparse low vegetation, essentially characterized by *Tridens pulchellus*
3. an upslope vegetation band densely covered by perennial grass *Hilaria mutica* in 15- to 60-cm-high tufts, under a dense shrub canopy of 1.0 to 1.5 m high, almost exclusively made up of *Flourensia cernua*
4. a floristically more diverse area, consisting of shrubs and a tree species (*Prosopis glandulosa*), from 1.5 to 2.5 m high, followed by open shrubland with fewer species and fading into a rim of old dying tufts of *Hilaria* and a few trees: in this zone, the finely structured soil had a high water permeability, due to the macroporosity caused by mesofaunal activity
5. a zone of bare ground covered by erosion crusts, with a few *Cactaceae* and remnants of dead shrubs

The soil did not show any discontinuities or marked pedological heterogeneity within the two-phase mosaic unit, except for some minor variations in the topsoil (0 to 30 cm) in relation to the plant cover. These variations involved the thickness of the horizons and the organic matter content of the top soil (Delhoume 1988). The slope was irregular and ranged from 0.7 to 0.9% in the transit zone, less than 0.4% in the pioneer zone, and intermediate in the vegetation formation (0.5 to 0.6%). Moreover, the existence of a microrelief (gilgai type) within the vegetation formations differentiated them from the bare zones.

Methods

Soil water content was monitored over a a 4-year period along a transect parallel to the slope and located across one bare area and one vegetation band. Access tubes for a neutron probe were installed to 1.20 m deep in six different locations. These corresponded to the five zones of the vegetation mosaic unit described above, plus an extra one in the rear edge of the dense shrub zone (listed as a separate functional zone in Table 5.1). Measurements were made every 10 days during the rainy season and every month during the dry season. To assess infiltration and runoff more precisely, extra measurements were made before and after 16 storms, which ranged from 7 to 67 mm in size. These data allowed dependable conclusions to be drawn on redistribution of water over the soil surface.

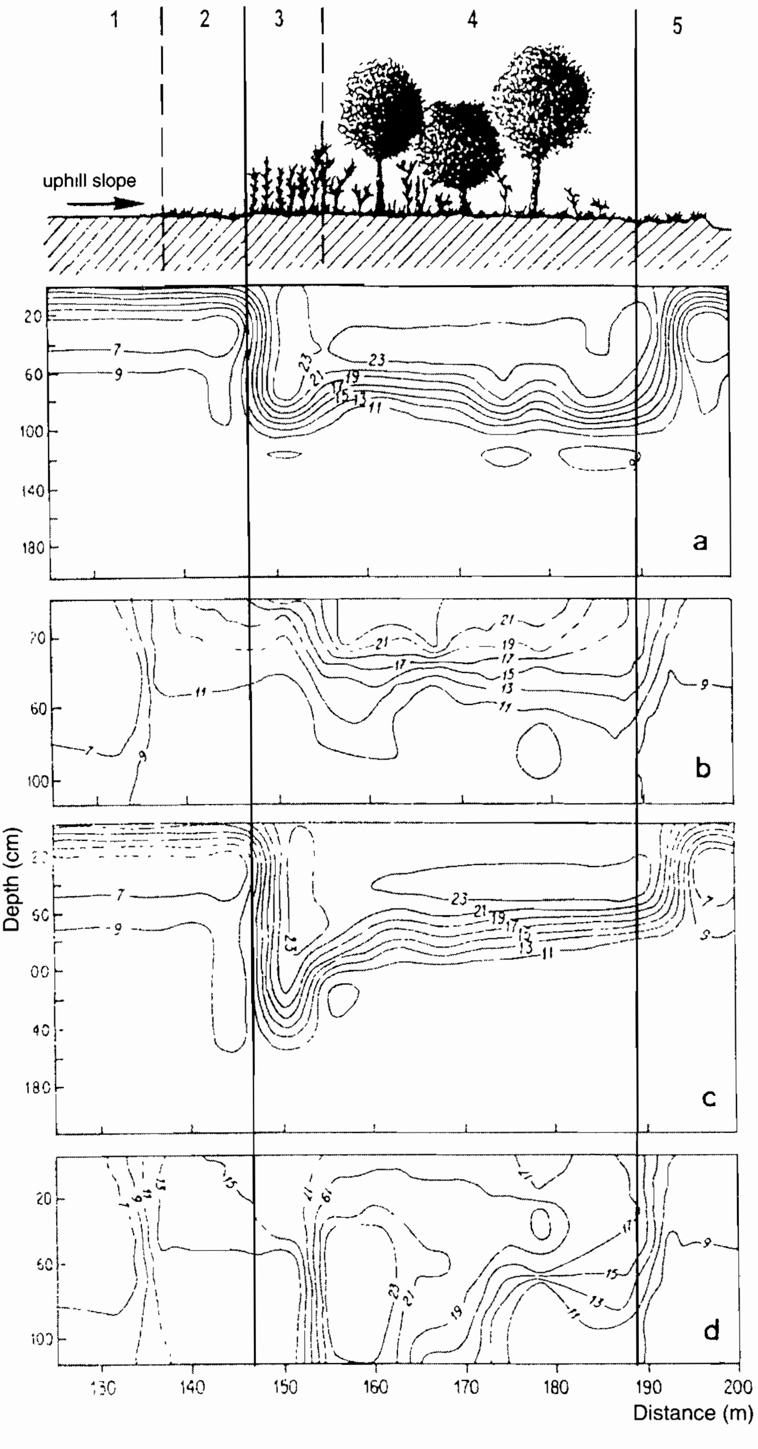

Figure 5.2. Water infiltration in the five zones of tiger bush (Mapimi, Mexico). (Modified from Delhoume 1996.)

Particular attention was paid to neutron moisture meter calibration. The high clay content of the soil (40 to 50%) dominated by smectites, produced cycles of swelling and shrinking. Delhoume (1988) had shown that the bulk density of the soil varied from 1.3 to 1.7 g cm^{-3} as the gravimetric water content varies from 0.32 to 0.05 g g^{-1}.

Quantitative Results Related to Soil Water Balance

The rainfall concentration factor (RCF; change in soil water storage divided by size of rainfall event) was plotted against rainfall for 16 events (Figure 5.3). An RCF of 100% indicates that infiltration equals rainfall. The RCF values of the three "bare" zones (upslope, central, and deposition area) were almost without exception less than 100%. This means that there was almost always net runoff from each of these zones. The two vegetated zones benefited from this additional supply of water and had RCF values of up to 300%. The RCF values were fairly stable for each zone for rainfall events exceeding 7 mm. The mean values of the RCF were 25% for the upslope and central bare area, 80% for the deposit area, 150% for the upslope vegetation zone, and 200% for the dense shrub area. Thus, runoff generated in upslope bare areas (75% of rain) crossed but did not infiltrate in the deposit area. Instead, runoff water infiltrated in the *F. cernua* zone to some extent and even more in the shrub zone. As observed in Australia, and despite its position downslope of the bare area, the deposit zone hardly benefited from the runoff.

This behavior has been simulated in two water-balance models (BIJOU and TLALOC), based on the water-balance equation (Eq. 5.1).

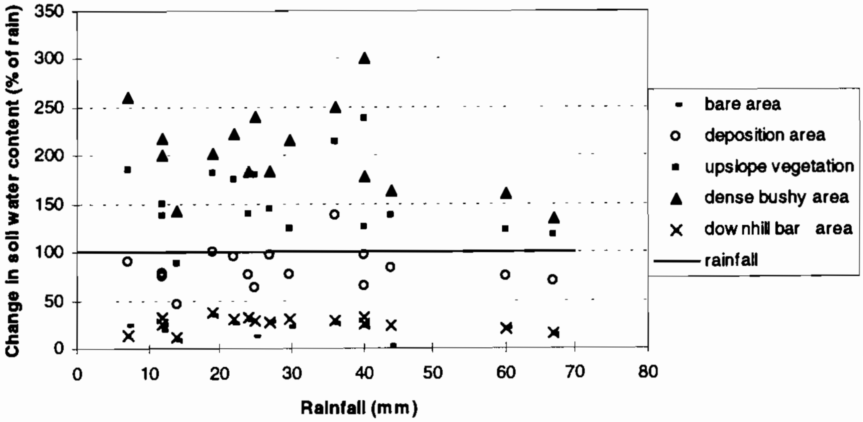

Figure 5.3. Mapimi (Mexico): Section across a vegetation stripe and location of the five functional zones. Associated patterns of soil water content variations after a low-intensity 33-mm rain (a and b) and after a 50-mm storm (c and d). For each rain, the simulated data are presented above the measured ones. (From Mauchamp, Rambal, and Lepart 1994.)

$$\Delta S = P - R - D - AET \qquad (5.1)$$

where

ΔS is the change in soil water content
P is the precipitation
R is the runoff (or runon)
D is the loss through drainage
AET is the actual evapotranspiration

This equation expresses conservation of water in each zone during a time-step. In Mapimi, D was assumed to be nil as the wetting front never passed the monitored depth (120 cm).

The BIJOU model (Cornet 1981; Cornet and Rambal 1981) estimates AET from the experimental relationship of Eagleman (1971), which used the PET values of Penman, the vegetation cover, and the relative soil moisture. After calculation of the AET value at each site, the R value was determined step by step so that the resulting water storage matched the measured storage (Cornet et al. 1992). The AET for the bushy area was about three times higher than the rainfall (Table 5.4) and matched its high measured infiltration (Figure 5.4). Moreover, in this zone, vegetation cover reduced losses through soil evaporation, and consequently the ratio of evapotranspiration to water supply was maximized.

The TLALOC model, developed by Mauchamp, Rambal, and Lepart (1994), takes into simultaneous account within-patch dynamics, ecotone dynamics, and the interactions between patches and flows. In each square meter of a transect perpendicular to a band, both functional and dynamic processes were simulated. In this section, we focus on the functional modeling of water balance of the TLALOC model. In this model, AET and R are simulated, and ΔS is the output that is compared with actual measurements. The runoff is assessed in each quadrat (1 m^2) by

Table 5.4. Calculated Values of the Water Budget Components (in mm) during the Period February 8 to September 9, 1985, in Mapimi (Mexico)[a]

		Upper bare zone	Upslope part of vegetation stripe
Rainfall (mm)[b]		227.7	227.7
Potential evapotranspiration (mm)[c]		1353	1353
Initial water storage (mm) 0–120 cm[b]		72.7	106.9
Final water storage (mm) 0–120 cm[b]		75.2	178.2
Actual evapotranspiration (mm)[c]		138.7	654.3
	(%P)	61%	287%
Runoff	(mm)[c]	+86.5	–497.9[d]
	(%P)	38%	219%

[a] From Cornet et al. (1992)
[b] Measured value
[c] Calculated value.
[d] Negative value corresponds to runon.

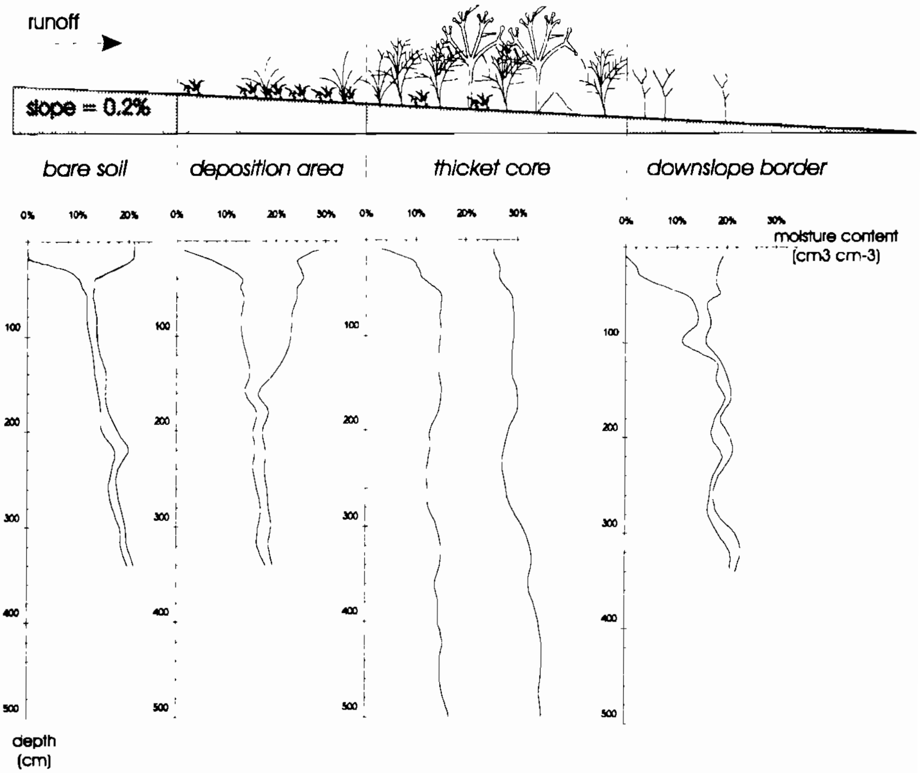

Figure 5.4. Annual range of variation in soil moisture content across a tiger bush unit. (From Galle, Seghieri, and Mounkaila 1997.)

using the USDA Soil Conservation Service method. Compared with the original equations (Boughton 1989), water input (*W*) is composed of rain plus runoff coming from the upslope quadrat. Only one parameter ($I_{VC(x)}$; a surface water storage or retention factor) is needed to assess the runoff of any quadrat (R_x):

$$R_x = (W_x - 0.2\, I_{VC(x)})^2/(W_x + 0.8\, I_{VC(x)}) \quad \text{for } W_x \geq 0.2\, I_{VC(x)} \tag{5.2a}$$

$$R_x = 0 \quad \text{for } W_x < 0.2\, I_{VC(x)} \tag{5.2b}$$

W_x is the water input = $P + R_{x-1}$
R_{x-1} is the runoff coming from the upslope quadrat
$I_{VC(x)}$ is the potential maximum retention of the quadrat, related to its vegetation cover (VC)
x is the quadrat position

Two parameters corresponding to bare soil ($I_{VC=0}$) and complete cover ($I_{VC=1}$) were determined from the infiltration measurements of Delhoume (1996). Any intermediate position was related to the percentage of VC by a sigmoidal curve. This method permits cover to evolve over time but does not assume landscape zonation. However, a realistic model should generate or maintain zonation. The remaining water was redistributed vertically within the profile by using a reservoir model. After rain, the AET consisted of evaporation and transpiration. The ratio of partitioning was linked to the VC. Evaporation was modeled with the Ritchie (1972) equation, transpiration using the function proposed by Feddes, Kowalik, and Zaradny (1978). This function needed a soil water retention curve, which is difficult to estimate, but the maximum depth reached by roots is a more important factor for which field measurements were available. The maximum root depth was 2 m for the trees.

Mauchamp, Rambal, and Lepart (1994) calculated the water budget for 13 years from initial in situ conditions. They found a mean runoff of 55% from bare zones (VC = 0). This percentage was reduced to 25% when a 50-m-wide vegetation band was assumed to be present. The system therefore was not closed for individual mosaic units so that water supply was higher for the bands lower in the landscape. This would explain the observation of Cornet and colleagues (1992) that the broadest bands are to be found in the lower part of the toposequence.

According to the model calculations, the annual soil water budget was stable: little change was observed in the soil water content from one year to another. The AET was found to be equal to infiltration. Modeled infiltration reached 300% of total rainfall in densely vegetated areas, 283% in the upper edge, 137% at the rear front, and only 52% in bare areas (Table 5.4). The average modeled infiltration rates were slightly higher than those measured. This was because the modeling included all rainfall events throughout the season, including those that produced no runoff but infiltrated 100%.

These patterns of rainfall redistribution within a two-phase mosaic unit may vary with the intensity of rainfall and with initial soil moisture content. A pronounced gradient of soil water content was simulated within the band after a heavy storm of 50 mm, but a more homogeneous water content was obtained for low-intensity rain (see Figure 5.2). Even though TLALOC overestimates the infiltration in the *F. cernua* zone, these results were in remarkable agreement with field data. Measured maximum infiltration rates were also found downslope in the dense shrub zone. Overall, it can be concluded that at Mapimi, too, the spatial and temporal water availability determined vegetation productivity and that among perennial vegetation, the shrubs in the central dense shrub zone were more sensitive to the benefits of runon than the grasses in the upslope vegetation.

Niger

Tiger bush patterned vegetation was first described in Niger by Clos-Arceduc (1956) based on aerial observations. This type of vegetation covers one-third of Sahelian Niger (between 400- and 700-mm annual rainfall). It occurs exclusively on plateaus, capped with a thick Pliocene ironpan (Gavaud 1965). The shallow (25 to 85 cm) gravelly soils have low plant nutrient status (Ambouta 1984) and are poorly developed.

Since 1992, hydrological and ecological studies related to tiger bush functioning were undertaken in Niger as part of two international experiments, HAPEX-Sahel[1] (Goutorbe et al. 1994) and GCTE-SALT[2] (Menaut, Saint, and Valentin 1993). Within these larger experiments, the tiger bush was studied intensively at two sites: near Banizoumbou, 50 km east of the capital Niamey, and near Say, 30 km south of Niamey (Figures 1.3a and b and 1.5, this volume). The common aims and soil water monitoring procedures are described by Cuenca and colleagues (1997). The annual potential evaporation is almost 2500 mm. Mean annual rainfall in the Niamey region for the period 1905 to 1989 was 560 mm, with a standard deviation of 140 mm (Lebel, Taupin, and d'Amato 1997). The year can be divided into a dry and a rainy season, with 75% precipitation falling between July and September. At this latitude, rainstorms are mostly convective and display high spatial variability at the event as well as the seasonal scale (annual rain CV = 26%). For example, during 1992 two stations less than 10 km apart recorded annual totals of 510 and 780 mm, respectively (Lebel and Le Barbé 1997).

Banizoumbou

Description

The Banizoumbou plateau is to the northeast of the Niger River and lies at about 250 m above sea level. The general slope of the plateau is about 0.2% (range, 0.06% to 0.5%) (Galle, Ehrmann, and Peugeot 1999). The study site comprised a typical tiger bush pattern with trees covering 25% of the area. Couteron and others (2000) studied the vegetation of this plateau along a 700-m-long transect crossing eight vegetated bands. They found that the average width of the perennial vegetation bands was 10 m (±7 m) and of the bare areas 50 m (± 28 m). The high variation was due to the undulating border of the thickets. The main woody species are *Combretum micranthum* G. Don and *Guiera senegalensis* J.F. Gmel., which average 2.40 m in height. The bands had distinct vegetation composition zones on an upslope-to-downslope gradient.

On a nearby site, Thiéry, d'Herbès, and Valentin (1995) observed that soils in and between vegetation bands showed few morphological differences, apart from those that can be directly accounted for by the influence of the vegetation itself (i.e., higher porosity and rooting within the vegetated bands). These observations are consistent with other soil surveys of Nigerian tiger bush (Ambouta 1984; Barker 1992; Bromley et al. 1997a). Although soil textural properties show few differences, the soil surface presents various types of crusts organised in a predictable succession along the slope, as described at Banizoumbou by Seghieri and co-workers (1996). The basic tiger bush unit was composed of a bare area with erosional crusts, changing to depositional crusts at its downslope edge, which merged into

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[1] HAPEX-Sahel: Hydrological and Atmospheric Pilot Experiment in the Sahel.

[2] GCTE-SALT: Global Change Terrestrial Ecosystems—Savane à Long Terme core project.

a shrub zone divided into two zones, the core and the downslope margin. The deposition area, covered by annual grass and sparse shrubs, was considered either as the downslope part of the bare area or an upslope border of the thicket, depending on authors.

Galle, Ehrmann, and Peugeot (1999) studied both water storage to a depth of 5.60 m and runoff on three plots of about 50 m^2. Soil moisture profiles were measured in two transects of neutron probe access tubes. Each transect, installed perpendicularly to a different vegetation band, included at least one access tube in each of the four zones of the tiger bush (Figure 5.4). Soil moisture profiles were monitored at a rain-dependent time-step (1, 2, and 4 days after rainfall). Measurements were progressively decreased to once monthly during the dry season. The observation period covered 4 years, including both relatively poor (–25%) and wet (+21%) rainy seasons.

Quantitative Results Related to Soil Water Balance

The measured infiltration showed sharp variations in the different landscape zones. The infiltration in the core of the band was rapid, and the wetting front passed 5.60 m during the rainy season, whereas it hardly reached 50 cm at the downslope edge of the band (Figure 5.4). Data from the runoff plots showed that on the three different crusted zones, runoff has a classic piecewise linear relationship with rainfall amount: no runoff is observed below a rainfall threshold, but above this value, runoff varies linearly with rain (Table 5.4; Galle, Ehrmann, and Peugeot 1999). There was a different rainfall/runoff threshold for the each of the three runoff generating zones. At the seasonal scale, runoff was 18% of annual rainfall on the downslope of band zone, 54% on bare soil, and 2% on the deposition zone. Galle, Ehrmann, and Peugeot (1999) tested this simple runoff model against soil water storage data. For 60 rainfall events over 4 years, changes in soil water storage, equivalent to infiltration, were compared with the difference between rain and estimated runoff (Figure 5.5). In the core of the band, the measured infiltration was reduced to 16 events, otherwise deep drainage occurred. The deposition area did not benefit from upslope runoff. Whereas in the core of the thicket, measured infiltration corresponded with the sum of the contributions of upslope zones, weighted by their relative lengths. Thus, the downslope border of the vegetated band contributed 10% of the adjacent thicket supply, the bare area 62%, the deposition area only 1%, and direct rain 27%. This means that the average water accumulation in the thicket equaled four times the incident rainfall. These significant additions of water in the thicket core explained the presence of two Sudanian woody species normally found in a more mesic climate (J. Seghieri, pers. comm.). However, as also observed in Mapimi, the water redistribution was not homogeneous within the core of the thicket. At the most favorable location (upper edge of the thicket core), infiltration depth was measured to be about eight times incident rainfall. The important runoff, mainly generated on the impervious bare area, crossed the deposition area without infiltrating to the entire benefit of the thicket core. The infiltration percentage measured in the deposition area was explained by

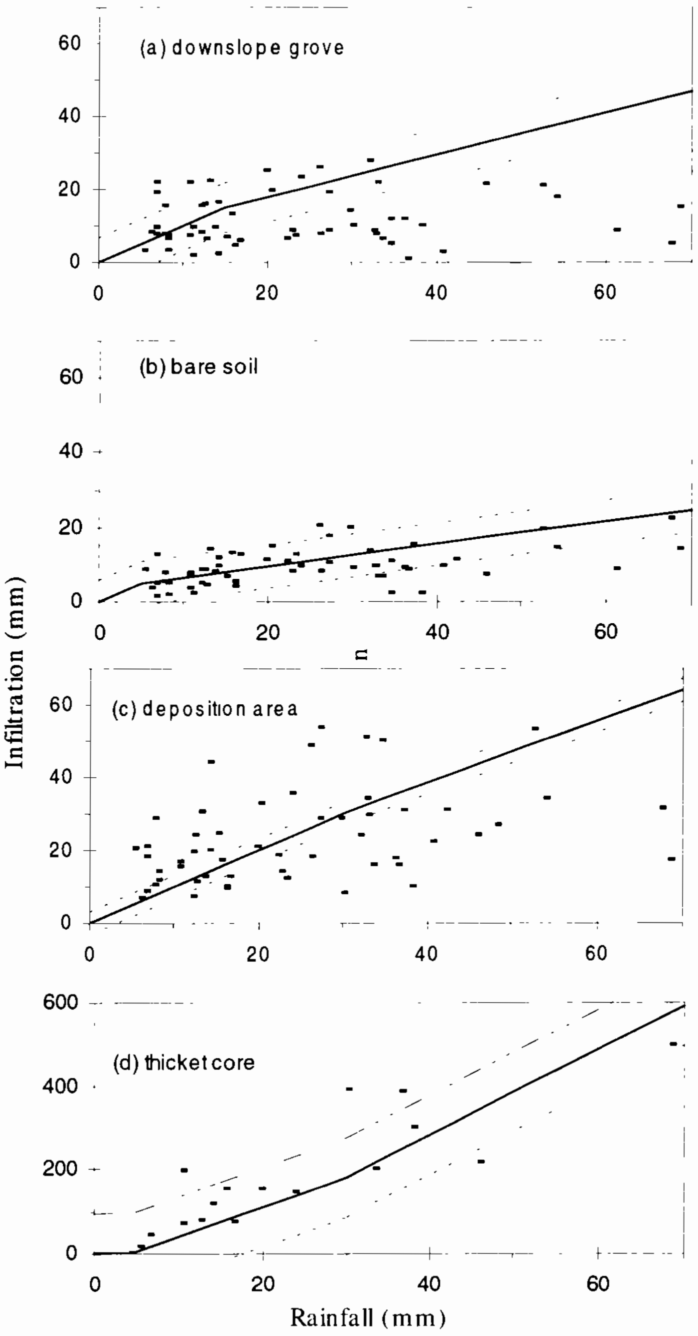

Figure 5.5. Observed and modeled change in soil water storage (infiltration) versus rainfall. (Reprinted from Catena 37, Galle, Ehrmann, and Peugeot, Water balance in a banded vegetation pattern, pp. 197–216, Copyright 1999, with permission from Elsevier Science.)

combination of its low microtopography and its low inherent infiltration rate. The natural obstructions caused by biological activity in the thicket core create a counterslope, so that water ponds upslope in the deposition area where sedimentation crusts were observed. However, infiltration rates in this zone were low (K_s = 1.8 mm h^{-1}) (Vandervaere et al. 1997), and the shallow depressions quickly overflowed into the core of the thicket where macropores permitted rapid infiltration under ponded conditions observed during rain. Little or no runoff was therefore available for the downslope border of the thicket, which was consequently only rain-fed. It should be added that the deposition area was the only zone to exhibit a cyclic seasonal trend in infiltration. By the end of the rainy season, it had enhanced macroporosity, due to annual vegetation growth and termite activity, and was able to infiltrate larger amounts of water from late rains.

To verify the conclusions regarding the importance of runoff for the survival of the bands of vegetation, a wall was built to prevent runon to the vegetation band (Seghieri and Galle 1999). The wall was located at the boundary between the bare soil zone and the upper edge of the deposition area. The difference in infiltration and in plant survival between the treatment and control confirmed that the overall runoff process advantaged only the core of the band during an average rainy season (about 560 mm). However, toward the end of a wetter rainy season (672 mm), the deposition area and downslope edges of the band also received extra water (Galle, Seghieri, and Mounkaila 1997). In the treatment deprived of runon, herbage growth was severely reduced in the deposition area, whereas only a smaller effect was observed in the thicket core. Here, the infiltration capacity was so high that even a reduction in water input (by a factor 8) could not induce a water deficit in the main rooting zone (0 to 1 m). Although strongly stressed, shrub species located in the deposition area survived a 45% reduction in water infiltration. The spatial organization clearly made the whole system resilient in the face of temporal rainfall variations (Seghieri and Galle 1999).

At Banizoumbou, Galle, Ehrmann, and Peugeot (1999) also noted that, although a single tiger bush unit acts as a source-sink system, at the plateau scale hydrological connections between intervening bare areas allowed some runoff from the plateau to take place. However, Peugeot and associates (1997) showed that the runoff over the edge of the plateau mainly comes from the bare border of the plateau.

Say

Description

The Say plateau is located on the southern side of the Niger River. Its vegetation and altitude are comparable with those of the Banizoumbou plateau. The tiger bush units were divided into four classes of vegetation, namely, bare ground, grassy open shrub (deposition area), closed shrub, and bare open shrub. This is similar to landscape zonation at Banizoumbou. Five transects of neutron probe access tubes were installed at right angles to vegetation bands. Tubes were installed to a depth varying from 1 to 6 m. The time interval between the measurements before and af-

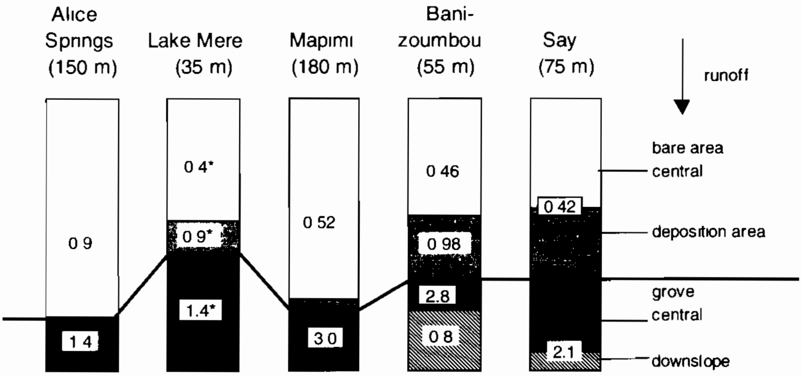

Figure 5.6. Rainfall concentration factor versus vegetation contraction on all studied sites. Lake Mere results (*) refer to a single 37-mm rainfall.

ter rain ranged from 1 to 3 days. Note, however, that relative proportions of each zone may vary with the site (Figure 5.6), which may be due to slight differences in ecological circumstances but also to the difficulty in clearly determining the boundaries of the zones. Most of the hydrological fieldwork was carried out during the 1992 rainy season (Bromley et al. 1997a).

Quantitative Results Related to Soil Water Balance

Observations revealed that runoff from bare areas began within minutes of the start of a rainfall event. The runoff reached the deposition area where the water tended to pond in slight depressions. The overflow from these depressions disappeared into the litter cover associated with the dense bush zone (Bromley et al. 1997a), as also observed at Banizoumbou by Galle, Ehrmann, and Peugeot (1999).

At –40-mm hydraulic potential, infiltrometer measurements showed similar infiltration rates and hydraulic conductivity on the bare soil, the deposition area, and the core of the thicket (Table 5.5). This reflects the similarity of the soil matrix or texture of all the zones of tiger bush. Ponded hydraulic conductivity for the bare ground and the deposition zones were similar to the –40-mm data, but the soil under the core of the thicket had an infiltration rate an order of magnitude higher, as also observed in Australia (see Table 5.2). Examination of the soil profile showed that in the core of the thicket, large pores (≤6 mm) perforate the soil surface. Dye tests revealed the presence of preferential flow along active and inactive root channels and termite tunnels, in addition to matrix flow (Bromley et al. 1997a).

Bromley and colleagues (1997a) calculated the rainfall concentration factor (the ratio of change in water storage to rainfall) for four rainfall events. The values obtained ranged from 22% in the bare zone to 350% in the deposition area. The average rainfall concentration factor was about 200% in the core of the thicket. These results were similar in principle but different in magnitude from those of Galle, Ehrmann, and Peugeot (1999). The differences may be related to the lower number of measurements at Say but also to differences in site organization. The bare

Table 5.5. Measured Surface Saturated Conductivity K of Different Surface Type in Say (Niger)[a]

	Matrix potential	
	−40 mm	−5 mm
Bare open bush (downslope grove)	12	9
Bare area (central bare area)	15	14
Grassy open bush (deposition area)	8	7
Closed bush (central grove)	6	37

[a] Modified from Bromley et al. (1997a).

zone–to–vegetation zone ratio was only 2 at Say, for instance, whereas it was 2 to 3 at Banizoumbou. Moreover, the drainage component was unknown at Say and may be important. It was not in Banizoumbou where such rain events were excluded. One cannot exclude also some geological differences between the two sites located on either side of the Niger River.

Culf and assoicates (1993) presented some measurements of the total evapotranspiration from the same tiger bush as Bromley and colleagues (1997a), including both bare and vegetated zones. When the soil was wet, Culf and associates (1993) measured maximum area average evapotranspiration rates of 5 mmd^{-1}. The total evapotranspiration of the 1990 season (428 mm) was estimated to be 97% of the rain ±10%, leaving little for runoff or recharge. Culf and colleagues noted the need to separately determine the evaporation from the bare soil bands. On the same site, Wallace and Holwill (1997) used the Bowen ratio energy budget approach to measure soil evaporation, placing the sensors close to the soil surface. They measured that the evaporation from bare areas decreased from 4 mmd^{-1} on the day following a rainstorm to 0.5 mmd^{-1} 3 days later (cf. results from Alice Springs in Figure 5.1). They calibrated the Ritchie (1972) approach with these data and simulated soil evaporation over an 11-year period. Annual evaporation came to 42% of rainfall when rainfall was close to the average of the area (560 mm) and markedly increased in drier years. For 1984, when rainfall was only 260 mm, they calculated that 79% of the rainfall evaporated. They estimated that bare soil runoff tends to zero when rainfall decreases to less than 200 mm yr^{-1}.

Conclusions

The studied sites show some common characteristics with respect to the soil water balance despite obvious site differences (see Table 5.2). First, all sites have a semiarid to arid climate, with potential evaporation much higher than annual rainfall. However, the total annual rainfall differed greatly from 250 mm in Alice Springs to 560 mm in Niger. All sites have some heavy rainstorms, but they are not necessarily restricted to a particular season: at Lake Mere, they can occur at any time of year. A significant part of the seasonal rainfall at all sites comes in small events: typically, 80% of annual total is in rainfall events of less than 10 mm. Thus, only a few rain events (four to eight per year) generate runoff and consequent water redistribution.

Slopes everywhere are gentle and never exceed 1%; thus, sheet runoff is the dominant process. The soil texture is not greatly different between band and interband at all sites, but soil surface crusting, porosity, and organic matter content vary markedly with cover.

For each zone at each site, the major results concerning infiltration for a mean year are summarized in Figure 5.6. On bare crusted soil zones, there is a threshold rainfall quantum varying from 4 to 15 mm (see Table 5.3) after which a large proportion of the rainfall runs off, except at Alice Springs, where only 20% runs off. This runoff transits the downslope bare area or deposition zone with no significant infiltration compared with the huge volumes of incoming water, which is composed of direct rainfall plus runoff from upslope. In Niger and Mexico at least, the downslope bare area is covered with sedimentation crusts, which result from deposition in standing water. The water tends to pond in slight depressions where fine particles deposit and the resulting infiltration rates are low (2 mm h^{-1} measured in Niger). Sedimentation crusts are rarely seen in Australia, where raindrop-induced crusts are common (D. Tongway, pers. comm.). Annual grasses and herbs and colonizing shrubs are found in this zone in Mexico and Niger. The overflow from these depressions disappears into the litter cover of the core of the band. Here, in contrast to bare crusted soils, there are macropores resulting from roots or bioturbation (observations from Lake Mere in Australia, Mexico, and Niger). Macroporosity plays a major role in water redistribution within the tiger bush unit as it facilitates rapid infiltration under ponded conditions, generally observed during rain. It has been shown in each continent that the soils have comparable infiltration rates on bare soil and vegetated bands for negative pressure head, when the soil matrix governs infiltration, but huge differences are observed under ponded conditions. The macroporosity of the shrub bands results in infiltration rates of four to 10 times greater than the bare/herbaceous areas. Within the vegetation band, infiltration rates are not homogeneous. Slatyer (1961) emphasized the role of roots or distance to a trunk. In Burkina Faso, Ouedraogo (1997) reported that infiltration rate was related to the distance from an active termite mound, with a maximum value observed for the maximum harvest activity of *Macrotermes* (5 to 10 m).

These hydrodynamic characteristics lead to marked contrasts in soil water storage within banded vegetation units. The rainfall concentration factor in the thicket core (infiltration in the vegetated band divided by rain) varied with the studied sites and was linked to the ratio of total to vegetated area (Figure 5.7). However, this was not the only factor. At Lake Mere in Australia and in Say and Banizoumbou in Niger, maximum use was made of rainfall (rainfall concentration equals vegetation concentration), whereas at Alice Springs, much water apparently is not used by the local vegetation. The low runoff coefficient of the bare soil in Alice Springs (20%) did not contribute a lot of water to the band, and there may have been a considerable amount of deep drainage under the bare areas.

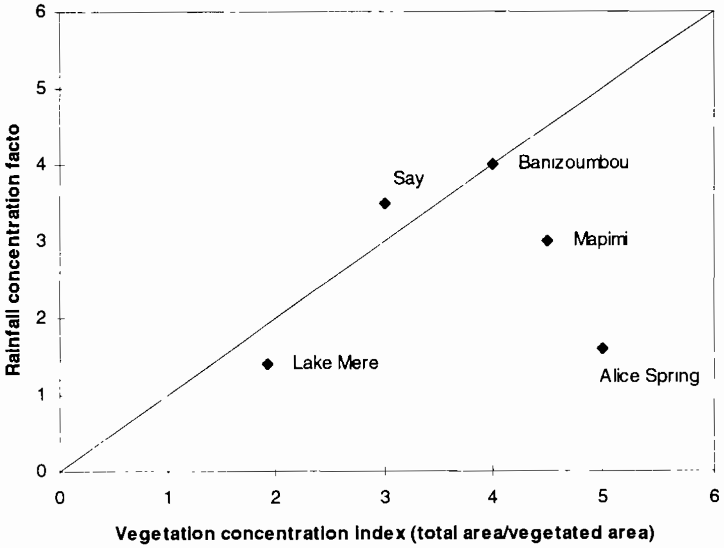

Figure 5.7. Percentage of each functional zone in a banded vegetation unit, for the five studied sites. Total length of a unit is noted in brackets. Total infiltration for average year (%P) is mentioned when available.

However, if the system is able to maintain all water resources within the banded vegetation unit, it should be well adapted to the climate. There have been some attempts to answer this question. At Lake Mere in Australia, Ludwig, Tongway, and Marsden (1994) showed that runoff from the system depends on the amount of annual rain. For a low-rainfall year, the bands retained all the incoming runoff water, but for years with mean rainfall, water left the system via runoff. In Niger, rain stayed in the source-sink unit, but deep drainage was observed in the soil profile, even during average years (Bromley et al. 1997a; Galle, Seghieri, and Mounkaila 1997). Wallace and Holwill (1997) estimated the recharge from modeled evapotranspiration measurements and arrived at an average figure for the site at Say of 3% of the average annual rainfall of 560 mm ±10%. This is equivalent to an average of 15 to 19 mm yr^{-1}. Bromley and colleagues (1997b) analyzed a 70-m-deep chloride concentration profile on the edge of a slight depression in a tiger bush area only 10 km from the site at Say described above. They found a mean recharge rate of 13 mm yr^{-1} (range, 10 to 19 mm or 2 to 3% of annual rainfall). For the total upland landscape in southwest Niger, including the valleys that separate different plateaus with tiger bush vegetation, regional recharge of the water table mainly takes place below gullies and pools and is about 10% of annual rain (Leduc, Bromley, and Schroeter 1997). In Mexico, although there was high runoff generated from the bare soil (75% of precipitation [%P]), the Mapimi site is clearly below the 1/1 curve (Figure 5.7). Mauchamp, Rambal, and Lepart (1994) calculated that 25% of runoff left the system, which was supported by field observations, in that the bands are wider in the downslope areas of the landscape, which receive the runoff. In summary, Nigerien tiger bush is about optimum for the actual climate: the hydrological contrast between vegetation and bare soil is high, with no runoff out of the system and little deep drainage (3%P). In Mexico and Australia, results are not so clear-cut because water does leave the system. However, the efficiency of the system cannot be reduced to simply the behavior in an average year, as high interseasonal rainfall variability (CV = 25%) is a characteristic of semiarid climates.

All reviewed studies of banded vegetation showed important changes in soil water balance of banded vegetation landscapes with the amount of annual rainfall. Continuing complementary studies (chapter 8, this volume) are using the functional TLALOC model (Mauchamp, Rambal, and Lepart 1994) to study a long time series including contrasting rainy seasons. This model, designed in Mexico, has also been tested on another site (Banizoumbou, Niger). The model accurately predicted the water redistribution in the different zones after the runoff module was slightly modified to take account of measured observations (Ehrmann 1999). The weakest point of the model is in the downslope bare area simulation, where infiltration and hence vegetation development are overestimated. The model could be improved by taking into account not only the overall amount of water but also runoff rate in relation to infiltration capacity of each quadrat of the tiger bush unit.

Global climate changes may affect the runoff/runon balance of the banded vegetation types discussed in this book. As an example, Culf and associates (1993) estimated that the Nigerien banded system could not function below 200 mm rainfall yr^{-1}. Increasing anthropogenic pressure could also modify the ecosystem function. Each reported study used as natural and undisturbed a site as possible. Scenarios of degradation or desertification have not been factored into the models yet. However, even low-density sheep grazing may significantly modify the functioning of banded vegetation as noted by Tongway and Ludwig (1990). In Niger, an additional fast-increasing pressure is the exploitation of tiger bush wood for domestic use (Peltier et al. 1995). Obviously, total wood exploitation would eventually generate high runoff (70% of rain exceeding 5 mm) through destruction of the sink areas, leading in time to disastrous erosion in the footslopes, as already seen in the Filingué region. Conversely, the maintenance of the bare areas in tiger bush is essential for the survival and productivity of woody vegetation as they bring 30 to 60% of the thicket water supply. Planting the bare zone with trees, as previously attempted in revegetation projects in Niger and elsewhere in West Africa, must be avoided.

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6. Soil Biota in Banded Landscapes

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and Paul Ouedraogo

Introduction

Patterned landscapes are characterized by the banding of perennial, usually dense vegetation on the contour, separated from more-or-less unvegetated soil. The vegetated section acts as a sink area, sequestering soil sediments, water, and nutrients shed from the bare source area immediately above it in the landscape. Water availability is the driving force in patterned landscapes, controlling the structure and the dynamics of the vegetation. Runoff generated on the source zones is trapped on the upslope areas of the sink zones where infiltration proceeds. At the same time, erosion of the lower surface of the vegetated zone is occurring so that the vegetated band gradually moves upslope (Ambouta 1984; Thièry, d'Herbés, and Valentin 1995). Given the importance of overland flow in the formation and maintenance of patterned vegetation, it follows that factors that influence the amounts and distribution of runoff and infiltration will ultimately affect the patterning phenomenon itself.

Soil biota are strongly influenced by water availability, and themselves influence critical soil and ecological processes through their effect on infiltration, soil physical and chemical properties, nutrient cycling, decomposition, and germination and establishment (Eldridge and Greene 1994; Whitford and Herrick 1996). Thus, soil biota have a controlling influence on the structure and patterns of the vegetation and the dynamics of the patterned system.

This chapter deals with the roles of soil biota, particularly micro- and macrofauna (protozoans, bacteria, ants, and termites) and microphytes associated with soil crusts (lichens, bryophytes, and cyanobacteria) in the initiation and maintenance of patterning in patterned landscapes and the management consequences thereof. Drawing on published and unpublished data, from mainly East and West Africa and eastern Australia, we discuss the distribution and structure of the communities comprising this biota in relation to soil and vegetation patterning. We examine their role in redistribution and cycling of scarce water and nutrient resources through their impact on primary ecological processes (particularly erosion and deposition); their role in soil physical and chemical processes (including soil structure, hydrological properties, and nutrition); their interrelationships with vascular plants (principally through their effect on germination and establishment), and their relationship to other soil biota. Finally, in the light of their roles in landscape development and the impact of various land uses such as grazing and the use of fire, we examine the role played by soil biota in assessment and monitoring of ecosystem condition.

Structure and Distribution of Soil Biota

Banded landscapes constitute an interesting model of a "self-modifying system" (Cornet et al. 1992), in which pattern results from complex interactions between primary and secondary ecological processes and landscape structure. In a general sense, these systems provide an excellent opportunity to examine ecological *process* through an understanding of landscape *pattern* (Smallwood 1993).

Soil Invertebrates

Microfauna: Protozoa and Nematodes

Desert soil protozoa are dominated by amoeboid forms (Whitford and Parker 1989), and ciliates and flagellates are less common (Parker, Philips, and Whitford 1984). These groups are patchily distributed and are strongly influenced by soil moisture. Their activity is limited to the periods when a film of microscopic soil water exists (Whitford and Herrick 1996). Therefore, when soils are dry they remain inactive as cystic forms (Parker, Philips, and Whitford 1984), often inhabiting the litter layer.

Given this sensitivity to both moisture and litter levels, it could be expected that greater abundance and diversity of microbiota would occur in the runon areas characteristic of banded landscapes, where soil moisture and plant and litter cover is enhanced, compared with the bare runoff areas. This variation in spatial distribution of microbiota has been recorded in the patterned woodlands of eastern Australia (Tongway and Ludwig 1990). Greenslade and Smith (1994), in a study of degraded areas in the same woodlands, showed that microarthropods responded to improved soil conditions encouraged by "re-creation" of fertile patches in the landscape. In their study, microarthropod density increased from 1400 m^{-2} in untreated plots to more than 5000 m^{-2} in treated plots.

Mesofauna (Microarthropods): Acari *and* Collembola

The dominant mesofauna in semiarid and arid systems are *Acari* (mites) and *Collembola* (springtails), although *Psocoptera* and *Diptera* larvae also occur (Wallwork 1976). In patterned landscapes, mesofauna generally occur in greater densities in the vegetated zones, which obviously provide appropriate food, habitat, and microclimatic conditions. Noble, Whitford, and Kaliszweski (1996) found significantly higher densities of mites, predominantly the prostigmatid and cryptostigmatid groups in the timbered groves of a semiarid patterned mulga woodland in eastern Australia, compared with other small-scale patches such as grass butts, mulga log mounds (Tongway, Ludwig, and Whitford 1989), termite pavements (Noble, Diggle, and Whitford 1989), or soil crusts. Increased densities in the timbered groves have been attributed to higher levels of litter and organic carbon content of the surface soils.

Macrofauna (Termites and Ants)

On a global scale, termites and ants constitute the dominant surface-active fauna in arid and semiarid tropical soils (Lal 1988). However, despite the extensive reviews dealing with the abundance and distribution of termites and ants and their nests in rangelands (Lee and Wood 1971, Lobry de Bruyn and Conacher 1990), there are few data specific to patterned landscapes.

All the main trophic groups of termites are represented in semiarid and arid areas. Without exception, these groups utilize dead plant material by forming symbiotic relationships with protozoa and bacteria. From those studies conducted in patterned eastern Australian woodlands, it would appear that termite densities are of a similar magnitude to those reported elsewhere. For example, densities of 350 to 1000 mounds ha^{-1} for subterranean *Drepanotermes* have been reported for the mulga communities (Watson and Gay 1970; Watson, Barrett, and Lendon 1978).

In a study of a patterned landscape in northern Burkina Faso by Ouedraogo and Lepage (1994), termite mound density was clearly related to the alternating pattern of the wooded bands and bare zones. Over the whole landscape, mean nest densities of *Macrotermes subhyalinus* was 8.4 ha^{-1}. However, live nests occurred mainly in the wooded groves where their densities reached 22.3 ha^{-1}. The present position of the eroded stages of *Macrotermes* nests (ranked from active to completely abandoned to eroded nests) showed that active nests were restricted to the wooded groves, whereas large numbers of abandoned eroded mounds were found in the bare intergrove areas. Their low densities in the groves is thought to be due to their inability to cope with inundation by runoff into the groves. In patterned eastern Australian woodlands, however, Noble, Diggle, and Whitford (1989) recorded higher densities of termite pavements in the runoff zones (100 ha^{-1}) compared with the timbered groves and drainage lines (30 ha^{-1}) where tree density is relatively high. This observation could be interpreted by the shifting upslope movement of the vegetated bands.

Apart from recent work by Bryannah (1995), there are few data on the abundance of ants and their nests in patterned landscapes or in semiarid and arid regions in general. Most data from patterned landscapes are anecdotal (e.g., Greene 1992), suggesting that ants are more common in the wooded groves compared with the bare runoff zones. In a patterned Australian woodland, Greenslade (1993) found that epigaeic species associated with grasses were more common in the groves. Similarly, abundance of both predatory and seed-harvesting ants (particularly the genus *Pheidole*) increased on areas treated with mulga branches, which simulate microgroves (Tongway, Ludwig, and Whitford 1989). Although total *Formicidae* increased on treated plots compared with nontreated plots (Greenslade and Smith 1994), increases in abundances of trapped ants was not reflected in increased densities of their nests, suggesting that the ants were foraging from areas outside of these plots.

Bryannah (1995) presented evidence for spatial variation in the abundance and diversity of the ant community in the same patterned woodland. Abundance, diversity, and species richness varied across the geomorphic gradient comprising bare stony runoff zones, grassy interception zones, and mulga grove runon areas. Variation across these zones was an order of magnitude greater than variation within zones, indicating a strong spatial element in variation of community composition coincident with geomorphic position. The pattern was strongly influenced by grazing, which influenced both the abundance and composition of the community across the geomorphic gradient.

Soil Crust Biota

Biological soil crusts are thin (<2mm) surface layers comprising a rich array of soil biota including cyanobacteria (blue-green algae), bacteria, fungi, eucaryotic bacteria, lichens, mosses, and liverworts. These crusts are differentiated from physical soil crusts (Valentin 1995) by being organogenic in nature, by their effects on infiltration and erosion processes (Eldridge and Greene 1994), and by their role in providing niches for soil fauna. Most soil crusts in arid regions are dominated by crustose and squamulose lichens, mosses, and some liverworts (Figure 6.1).

Biological soil crusts are a common component of soil surfaces in most semiarid and arid landscapes including patterned landscapes. In patterned stony downs systems (Dunkerley and Brown 1995), mosses and lichens cover less than 5% of the surface area of the landscape and are restricted almost entirely to the upper and lower slopes of the vegetated shrub bands, where they are protected by perennial shrub hummocks. Thièry, d'Herbés, and Valentin (1995) identified this zone as that where pioneering vegetation establishes. Sparse mosses, particularly the ubiquitous *Bryum pachytheca* and *Didymodon torquatus*, occur in the runon zone (Eldridge 1999). Individual thalli of the lichens *Peltula patellata* spp. *australiensis*, *Heppia despreauxii*, *Endocarpon* spp., and *Catapyrenium* spp. occur between the quartz gravel in the runoff zones (Eldridge 1999). Because cover levels are high, the potential for nitrogen fixation is high, due to nitrogen-fixing photobionts in the lichens. The vagant (mobile) lichen *Chondropsis semiviridis* tends to accumulate in patterned groves of belah-rosewood (*Casuarina cristata-Alectryon oleifolius*) in southeastern Australia because of the low frequency of threshold wind velocities required to move these lichens (Eldridge and Leys 1999).

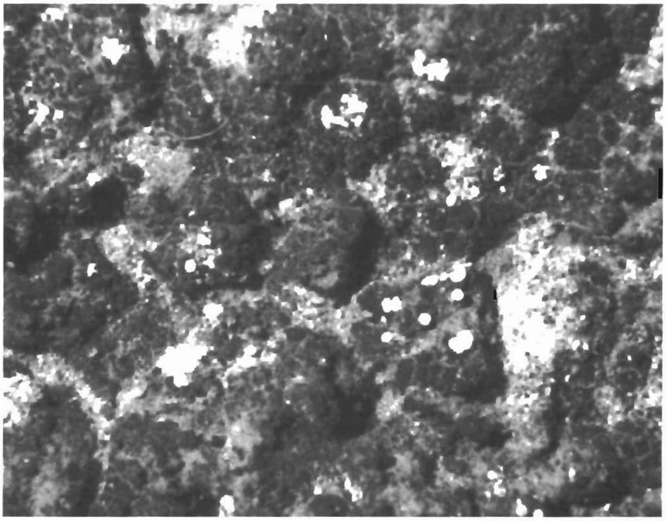

Figure 6.1. A typical lichen-dominated soil surface in the patterned semiarid woodland. These lichens increase soil aggregation and contribute to soil microtopography.

Crust cover in the patterned mulga woodlands is sparse, ranging from 2.3 to 8.8% in the mulga groves to 3.0 to 4.0% in the runoff zones (Ludwig and Tongway 1993; M.E. Tozer and D. Eldridge unpublished data). The dense vegetation cover in the mulga zones provides few opportunities for colonization by soil crust biota, except in relatively open groves. Here open spaces are dominated by bryophytes, particularly the mosses *Bryum pachytheca, Didymodon torquatus,* and *Goniomitrium enerve,* and the liverwort *Riccia limbata,* with few if any lichens. The runoff zones, however, supported a rich suite of crustose and squamulose lichens, particularly members of the genera *Endocarpon, Peltula, Psora, Catapyrenium, Buellia, Lecidea,* and *Acarospora.* In a study of patterned *Acacia aneura* woodlands in southwestern Queensland, Australia, Tozer and Eldridge (unpublished data) demonstrated major differences in crust species between the mulga groves and the runoff areas. Crust cover, numbers of species per plot, and species richness were greatest in the groves compared with the runoff areas. Most of this difference was due to bryophytes (particularly *Riccia* spp.) in the groves, whereas lichens, particularly *Peltula* and *Heppia* spp., were more common in the runoff areas.

Apart from lichens and bryophytes, patterned landscapes support a rich assortment of cyanobacteria (blue-green algae), bacteria, and fungi (Malam Issa et al. 1999). *Microcoleus vaginatus* is a common nitrogen-fixing cyanobacteria over extensive areas of arid and semiarid Australia (J. Belnap, unpublished data). Preliminary investigations in the mulga woodlands suggest a strong relationship between fixation rates and grazing rate, with crusted soils supporting four times the cyanobacterial biomass compared with crust-free soils (J. Belnap, pers. comm.)

Roles of Soil Biota in Ecological Processes

Soil biota can be viewed as *ecological engineers* (Lawton and Jones 1995) in that they actively modify their physical and chemical environment. In the arid and semiarid rangelands, soil invertebrates and microphytic crusts do this by affecting the movement of soil and water in the environment, nitrogen cycling, and germination and establishment of seedlings.

Pedological Processes

Soil-dwelling fauna affect pedological processes through two main processes (Lee 1992). These are *modification of soil profiles* (through burrowing and nest construction) that affect aggregation, structure, texture, porosity, and infiltration characteristics of soil; and *soil nutrition,* through the decomposition of organic matter and cycling of available nutrients through the soil profile.

Soil Profile Modification

In West African landscapes, soil accumulation and turnover by the termite *Macrotermes bellicosus* has been estimated at 1.5 to 2.0 mm yr^{-1} (Lepage 1984). Soil-covered runways used by termites also contribute significant amounts to pedoturbation. Of the 2 Mg ha^{-1} of soil brought to the surface annually by *Macrotermes subhyalinus* in Senegal (Lepage 1974), 675 to 950 kg ha^{-1} was contained in foraging runways on the soil surface. In East Africa, soil used in runways was about 1 Mg ha^{-1} yr^{-1} (Bagine 1984). In eastern Australia, termite sheeting was shown to be significantly more abundant in the mulga groves (6.6%) compared with the intergrove runoff zones (2.3%) (Whitford, Ludwig, and Noble 1992).

Soil transported by termite activity generally contains higher proportions of clay and silt particles (Hesse 1955; Boyer 1973; Pomeroy 1978). In their study of *Macrotermes* nests in Yatenga (northern Burkina Faso), Ouedraogo and Lepage (1997) describe a textural gradient in termite mounds, depending on degree of erosion and position within the mound structure. The mound center contained more than 50% clay, the mound wall 40% clay, and the erosion cone 20 to 30% clay, compared with less than 10% clay in the surrounding (control) soil. As the mound dies and is eroded, the surrounding soil is enriched with clay. Exceptions to this are found in the patterned eastern Australian woodlands, where the higher proportions of sand and lower proportions of silt and clay on termite mound soils compared with surrounding soils (Tongway, Ludwig, and Whitford 1989). This higher proportion of sand is attributed to aeolian and fluviatile processes as well as termite activity.

Ants generally transfer coarser subsoil material to the surface during nest construction, and Australian studies indicate that they can completely modify the surface 30 cm within 200 to 430 years (Humphreys 1981; Eldridge 1993). At Lake Mere, *Melophorus bagoti* was observed placing clay materials from nests at the base of perennial grasses some distance from the nest entrance (Bryannah 1995). Although this behavior is probably driven, in the ants, by the need to keep the nest entrance opening unobstructed, it has the benefits to plants of direct placement of nutrient-rich materials in a size class that would be easily dissolved by light rain or dew.

Although there are no empirical data for patterned landscapes, microbiota such as lichens and bryophytes act as sinks for wind- and water-detached sediments. The deposited soil is partly stabilized by protonema and the fine roots of desert mosses (Scott 1982; Danin and Ganor 1991) or by well-developed lichen rhizines (Eldridge and Greene 1994).

Soil Aggregation and Bulk Density

In the patterned mulga woodlands, Greene (1992) showed that aggregation in the top 10 mm of the surface was significantly higher in the timbered groves compared with the runoff and interception zones. The upper surface layer in this zone is characterized by an accumulation of organic matter and enhanced invertebrate activity and includes areas of microphytic soil crust. Termites influence soil aggregation by incorporating organic polymers with inorganic soil particles, thereby modifying the physical properties of the soil. However, although higher percentages of water-stable aggregates have been recorded in termite-inhabited compared with termite-free soils (Lobry de Bruyn and Conacher 1990), overall aggregate stability depends on the biology of the particular trophic group, with humivorous termites being more effective than fungus-growing termites (Garnier-Sillam 1989). Abandoned termite mound material generally has higher bulk density and lower porosity due to its compacted nature. Active feeding galleries, however, have high levels of porosity and, therefore, higher infiltration rates.

In a general sense, soil crusts increase soil aggregation through their association with hyphae-producing mycorrhizal and saprophytic fungi (Whitford and Herrick 1996) and free-living cyanobacteria such as *Microcoleus vaginatus* (Belnap and Gardner 1993). Fungal hyphae and cyanofilaments bind microaggregates (<250 µm) into water-stable macroaggregates through the production of microbial polysaccharides and gels (Chaney and Swift 1986). Aggregates from surfaces with microbiotic crusts are generally more stable than those from bare surfaces (Greene, Chartres, and Hodgkinson 1990). Current results from the patterned mulga woodlands (J. Belnap, pers. comm.) indicate that *M. vaginatus* is more influential in the runoff zones, where vascular plant cover is sparse.

Soil Hydrological and Erosion Processes

Soil hydrological processes are the principal factor contributing to the genesis and maintenance of patterned landscapes. Soil biota are involved in and influence these processes through their activities at the soil–air interface and in the upper soil horizons.

Infiltration and Runoff

Mounds of fungus-growing termites (*Macrotermes* spp.) are a conspicuous feature of patterned landscapes in Africa. *Macrotermes* spp. build specialized structures such as tunnels, galleries, and soil sheetings during foraging and feeding activities, which markedly affect water movement in these soils. Adult nests develop an underground system of tunnels and storage pits, and in a semiarid Kenyan savanna, these tunnels may occupy more than 20 km ha^{-1} at a volume of 4.5 m^3 ha^{-1} (Darlington 1982). Underground passages emerge through foraging holes at the surface. In these systems, termite activity is highly seasonal, ranging from 22,000 foraging holes per nest in the rainy season to more than 50,000 in the dry season (Lepage 1981).

In patterned landscapes, the number of foraging holes clearly varies across runoff and vegetated zones. This foraging activity also seems to be enhanced by the soil water status, as a wooded area, protected from runoff, exhibited a higher activity (540 holes m^{-2}) compared with the control areas (335 holes m^{-2}). This activity enhances the infiltration characteristics of the soil. Given the importance of macropores for conducting water into the subsoil, it follows that termite foraging areas are likely to have greater infiltration than termite-free areas (Figure 6.2). In

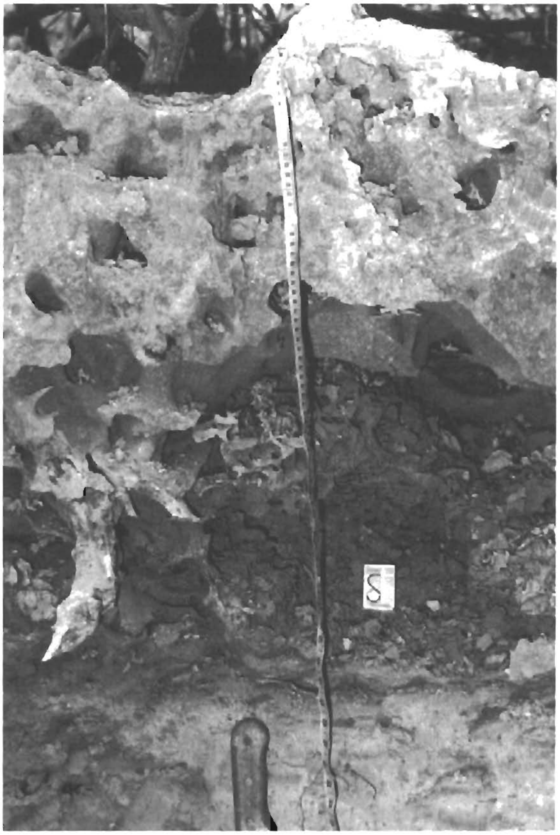

Figure 6.2. Cross-section through an active mound of *Macrotermes subhyalinus*. Note the large channels and storage galleries.

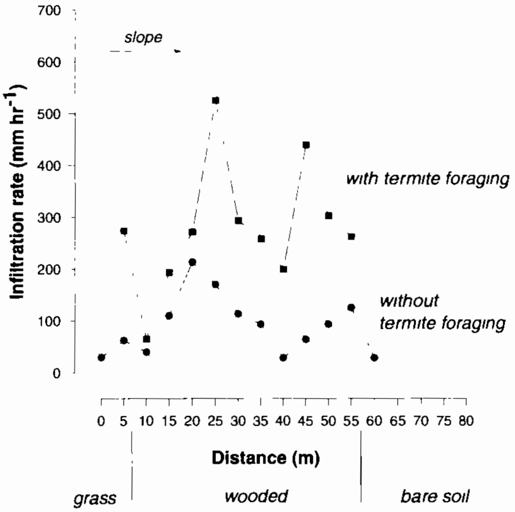

Figure 6.3. Variations in infiltration rate I_{30} (mm h^{-1}) across a catenary sequence of grassed, wooded, and bare soils with and without termite foraging. (I_{30} is the amount of water infiltrated after 30 minutes.)

the northeast of Ivory Coast, C. Valentin (pers. comm.) measured a fourfold increase of infiltration rate within termite foraging areas, as compared with unaffected soils. In northern Burkina Faso, Ouedraogo (unpublished data) measured the amount of water infiltrating into termite and termite-free soils over 30 minutes (I_{30}). I_{30} rates were five times greater in the foraging areas (336.2 mm h^{-1}) compared with the termite-free areas (72.6 mm h^{-1}). Differences in infiltration rates throughout the vegetation zones are shown in Figure 6.3.

In the patterned mulga landscapes, Greene (1992) demonstrated 10 times higher infiltration rates in the mulga groves, due to the presence of both termite and ant macropores. At a similar scale, Eldridge (1994) demonstrated 10-fold increases in infiltration in the annular zone of *Drepanotermes* spp. nest pavements, due to the greater number of macropores extending to the surface in this zone. The predominance of matrix- or micropores compared with macropores is responsible for greater runoff from mound soils compared with foraging areas (Lal 1988). Ouedraogo (unpublished data) found a 97.7% runoff on a dead unvegetated termite mound, compared with 82.2% runoff on a bare soil of similar size. The dynamics of runoff over time was markedly different between the two areas (Figure 6.4).

Little is known of the role of ant nest structures in patterned landscapes in relation to infiltration and runoff. Studies by Bevan and Germann (1982) and Lobry de Bruyn and Conacher (1994) in other semiarid systems stress the importance of macropores in water infiltration, but estimates of nest entrance (biopore) densities in soils affected by ants are few (e.g., Lobry de Bruyn and Conacher 1994). At a

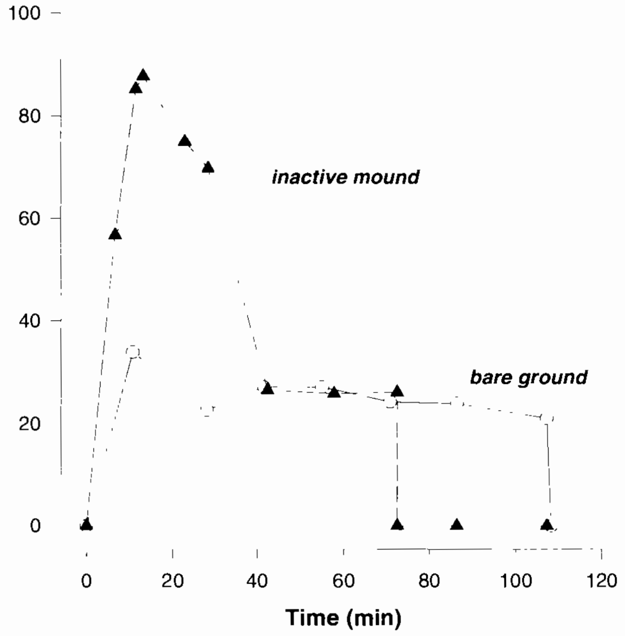

Figure 6.4. Changes in runoff rate (cm^3 mm^{-1}) on bare soil and an inactive termite mound.

finer scale of patchiness, Eldridge (1993) demonstrated a 10-fold increase in infiltration on soils occupied by entrances of *Aphaenogaster barbigula* compared with nest-free soils. He concluded that patchiness in such landscapes was accentuated by the activities of these soil-dwelling macroinvertebrates (Figure 6.5).

The role(s) of microbiotic crusts in infiltration processes is diverse and somewhat contradictory (West 1990; Eldridge and Greene 1994). Increased infiltration on soils with crusts has been attributed to enhanced soil aggregation, whereas decreases have been linked to hydrophobicity created by fungal hyphae and the blockage of matrix and micropores by fungal hyphae and rhizines.

Eldridge (1993) examined the role of crusts in infiltration processes on a patterned woodland in eastern Australia. The site comprised a mosaic of bare stony runoff zones (20 to 30 m across) supporting sparse ephemeral grasses and timbered groves (to 5 m across) supporting dense cypress pine (*Callitris glaucophylla*). In the vegetated runon zones, both sorptivity and steady-state infiltration increased markedly with increases in cover of microphytic crusts. However, in the runoff zones, there was no effect of crust cover on either sorptivity or infiltration. Overall, sorptivity was significantly lower on the runoff zones than in the vegetated zones. On similar soils patterned at a scale of tens to hundreds of meters, Greene and Tongway (1989) showed that highest infiltration rates corresponded with those sites supporting the greatest crust cover.

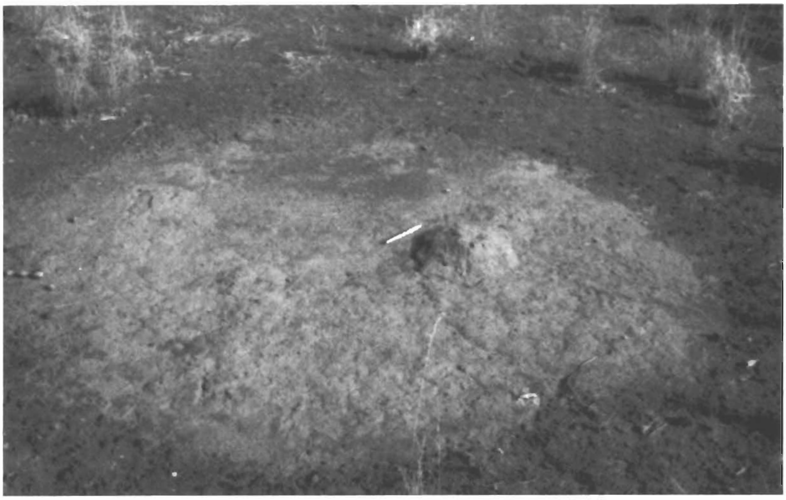

Figure 6.5. Ants contribute to small-scale patchiness around their nest, and their foraging may assist in dispersal of vascular plant seeds.

Differences in infiltration between different zones and surfaces may relate to differences in crust composition. For example, mosses trap water by using specialized leaf structures such as lamellae and filaments, channeling this water into the interior of the plant (Catcheside 1980). Lichens may influence increasing the availability of entry points for water into the soil by helping to stabilize fine matrix pores at the surface (Eldridge 1993).

Wind and Water Erosion

Foraging galleries of termites are easily entrained in stem-flow water and into overland flow. This may be a significant contribution to suspended sediments in runoff water moving through the groves and may contribute greatly to soil turnover in the groves. Little is known about the impact of soil biota on wind erosion. However, water erosion on clay-rich mound structures often leads to the formation of crusted surfaces, resulting in higher runoff rates, as is evident on *Macrotermes* spp. mounds. The development of a compacted plasmic crust may protect the underlying soil from further erosion by wind and water (Valentin, Collinet, and Albergel 1994). Soil eroded from *Trinervitermes* spp. nests may increase runoff long after a colony has been abandoned (Janeau and Valentin 1987). As mound turnover is slow, ranging from 10 years for *Cubitermes* spp. (Aloni and Soyer 1987) to 15 to 25 years for *Trinervitermes* spp. (Janeau and Valentin 1987) and more than 25 years for *Macrotermes bellicosus* (Lepage 1984), *Drepanotermes rubriceps*, and *D. perniger* (Watson and Gay 1970), the eroding mound material may continue to modify local drainage patterns for many years.

In a general sense, the beneficial role of crusts in reducing water and wind erosion in arid and semiarid systems is well documented in the literature (Collinet and Valentin 1979; Mucher et al. 1988; Kinnell, Chartres, and Watson 1990; Valentin and Casenave 1990; Eldridge 1993; Eldridge and Greene 1994; Leys and Eldridge 1998). Removal of this crust through trampling has important implications for soil hydrological and physical processes. In West African rangelands, cyanobacterial crusts may lead to the local strengthening of structural crusts, protecting them from further erosion (Valentin 1995; Malam Issa et al. 1999). They also form pedestals that have greater stability than uncolonized or eroded crusts (Casenave and Valentin 1989). Althoughwe are unaware of any erosion research pertaining directly to crusts in patterned landscapes, it is reasonable to assume that crusts reduce wind and water erosion in these systems, probably by enhancing surface roughness and by providing a physical barrier on the soil surface.

Soil Nutrition

Soil nutritional processes mediated by meso- and macroinvertebrates include decomposition, nutrient immobilization and mineralization, storage and release of water and nutrients, and nitrogen fixation (Whitford and Herrick 1996). Similarly, the cyanobacterial components of microphytic crusts play an important role, primarily in nitrogen fixation.

Termites and, to a lesser extent, ants consume large quantities of organic material. In the Sahel, termites have been shown to process up to 50% of the total aboveground primary production in some areas (Lepage 1974). In the semiarid area of the Tsavo National Park in Kenya, 90% of dead wood decomposition is performed by fungus-growing termites over a 10-year period (Buxton 1979).

Cyanobacterial sheath material probably constitutes a source of nitrogen for soil invertebrates and is, therefore, removed through this form of utilization. In some North American deserts, however, where microbial breakdown is slower, abandoned sheath material gradually accumulates in the soil, enhancing cation exchange, water-holding capacity, and stability of the soil surface, providing levels of disturbance are low (Belnap and Gardner 1993). Both cyanobacteria and sheath material are readily destroyed by fire.

Mineralization and Decomposition of Organic Matter

Rates of decomposition and mineralization are regulated by interactions between soil biota and by abiotic factors such as moisture, temperature, soil chemistry, and soil structure (Whitford and Parker 1989). Microarthropods are major regulators of carbon mineralization in decomposing litter (Parker, Philips, and Whitford 1984) and are active in even extremely dry soils. When microarthropods are removed with the use of biocides, carbon mineralization is closely reliant on soil moisture (Parker, Philips, and Whitford 1984).

In semiarid and arid ecosystems, termites enhance mineralization within their guts or within their nests, when high outside temperatures and drought preclude normal mineralization activity. Consequently, fungus-growing termites are able to process large quantities of litter despite unfavorable conditions. In northern Burkina Faso, Ouedraogo (unpublished data) studied the influence of soil reworked by termites on soil metabolism (carbon mineralization), by measuring carbon dioxide release under conditions of controlled temperature and humidity. Mineralization rates depended on the position in the mound and the structure of the eroded material and was up to four times greater in the mound wall and erosion cone compared with termite-free soils. Mineralization declined as the mound eroded, and abandoned mounds had very low levels. This work suggests that old *Macrotermes* spp. mounds may be unsuitable sites for the establishment of vegetation given their depleted nutritional status. In the active stages, however, release of organic matter from termitaria creates patches of nutrient-rich soil, leading to the development of landscape heterogeneity. It follows then that areas with greater density of termitaria (e.g., runon or timbered areas) will have higher net input of nutrients (Noble, Diggle, and Whitford 1989; Ouedraogo and Lepage 1994).

Nitrogen Cycling

Interactions between fungi, bacteria, protozoa, nematodes, and mites are complex. For example, Ghabbour and associates (1980) showed that protozoa and nematodes stimulated nitrogen fixation by cyanobacteria, despite a reduction in biomass of cyanobacterial crusts.

On patterned mulga landscapes, Tongway, Ludwig, and Whitford (1989) showed that termite mound soils contained significantly larger quantities of total and mineralizable nitrogen than surrounding soils. Unlike termites, which "lock up" their nutrients in long-lived mounds, ants may accelerate the cycling of nutrients through higher nest turnover. For example, Davidson and Morton (1981) showed that the nests of *Rhytidoponera mayri* in a patterned central Australian chenopod shrubland contained 100 times more inorganic nitrogen than surrounding soils.

The cyanobacterial components of lichen and algal crusts are often the single largest sources of nitrogen in semiarid and arid systems (Metting 1991), and in the absence of microarthropods, most nitrogen fixation in deserts and semideserts probably occurs in the context of symbiotic relationships between bacteria or cyanobacteria and lichens (Sprent 1985). Fixation rates of up to 100 kg N ha^{-1} yr^{-1} have been reported in the literature (Rychert et al. 1978), and although much of this nitrogen may be lost through volatilization and denitrification (Skujins and Klubek 1978), incorporation of biologically fixed nitrogen has been demonstrated (Harper and Pendleton 1993).

As nitrogen fixation is strongly tied to soil moisture, vegetated zones with higher levels of plant cover (and thus reduced evaporation) would be expected to have greater rates of fixation. In the patterned mulga woodlands of eastern Australia, the nitrogen-fixing photobionts *Scytonema* and *Nostoc* are associated with the ubiquitous lichens *Peltula*, *Heppia*, and *Collema* across all three landscape zones. Fixation rates are depressed when soil surface temperatures rise above approximately 50°C, a typical summer-spring daytime temperature in areas of full sunlight (i.e., runoff zones). As fixation is limited by low moisture availability, maximum nitrogen fixation probably occurs in runon areas. This is consistent with the observations of higher soil nutrient pools in vegetated runon areas compared with bare runoff areas (Tongway and Ludwig 1994).

Interactions with Vascular Plants

The concentration of nutrients by termites and, to a lesser extent, ants may be primarily responsible for the heterogeneous pattern of plant distribution characteristic of banded landscapes (Whitford and Herrick 1996). Seed dispersal by ants is another area of interaction between ants and plants, especially in arid ecosystems (Andersen 1991).

Germination of Seeds and Establishment of Seedlings

Numerous studies have described the vegetation associated with termite mounds in all kinds of ecosystems. In fact, the term *Termitensavannen* was coined by Troll (1936) to describe ecosystems in Africa that are characterized by discrete islands of woodland growing on large termite mounds, surrounded by sparsely wooded grassland (Lee and Wood 1971). Although there are detailed studies for many parts of the semiarid zone (see Malaisse 1985), few studies relate specifically to patterned landscapes.

Noble, Diggle, and Whitford (1989) presented evidence of enhanced grass (*Amphipogon caricinus*) establishment on the periphery (annular zone) of convex soil hummocks created by subterranean termites in a patterned mulga woodland. This was attributed to enhanced soil moisture through runoff and enhanced levels of both nitrogen and phosphorus (Spain and McIvor 1988). Concave mounds, however, generally restrict pasture growth, and although the surface may appear friable, it is generally overlain by structureless material of low hydraulic conductivity. Colonization of these sites therefore probably necessitates destruction of the pavement and rejuvenation of the underlying soil (Noble, Diggle, and Whitford 1989).

Ouedraogo (1992) demonstrated higher densities of trees and shrubs on mounds (2859 ha^{-1}) compared with nonmounds (527 ha^{-1}) in northern Burkina Faso. Although mound soil covered only 2.7% of the area, it supported 8.2% of the trees. Tree species closely related to mound soils included *Acacia ataxacantha*, *Boscia angustifolia*, *B. senegalensis*, and *Grewia bicolor*. Other species exhibited lower preferences such as *Combretum micranthum* and *Pterocarpus lucens*. Few others seem to avoid termite soils such as *Guinnea senegalensis*. Tree diversity was higher on the mound soils.

Generalist omnivorous ants play a major role in seed dispersal by harvesting the seed for the aril (food body) and later discarding the seeds with embryos intact.

The placement of these seeds in suitable microsites may eventually influence the chances of germination and establishment of seeds. In Australia, up to 50% of the flora is ant dispersed. Further work is required to determine the impact of seed harvesting on the population and spatial distribution of plants in patterned systems.

The relationships between microbiotic crusts and vascular plants are poorly understood. Some studies have reported positive associations between crusts and vascular plants, whereas others report negative associations (West 1990; Eldridge and Greene 1994). However, as crusts concentrate the two essential resources necessary for plant growth (water and nutrients) within the surface 10 mm (Graetz and Tongway 1986), it is conceivable that they have an effect on vascular plants (Eldridge and Greene 1994) if only in a spatially nonspecific way. Although there are some data reporting increased germination and establishment of vascular plants in the presence of microphytic crusts (Harper and St. Clair 1985; Harper and Marble 1989), we are unaware of any data relating directly to patterned landscapes. However, because microphytic crusts retain soil moisture, enhance soil nutrition, and elevate soil temperatures, they may enhance germination and establishment, at least in the initial growth stages.

Interactions Among Soil Biota and Soil-Dwelling Biota

Soil biota tend to be concentrated in areas of enhanced soil moisture, soil nutrients, and favorable soil physical properties and, at a landscape scale, favor runon areas, or nutrient-rich patches such as termite pavements and log mounds (Noble, Diggle, and Whitford 1989; Tongway, Ludwig, and Whitford 1989). Mulga log mounds in the patterned woodlands of eastern Australia support elevated populations of micro- and mesofauna such as *Amitermes* spp., which favor the surface of logs, and *Drepanotermes perniger* and *Tumulitermes tumuli,* which live inside the logs (Tongway, Ludwig, and Whitford 1989). Log mounds probably also act as refugia for plants and small animals such as lizards (e.g., *Ctenotus leonhardii*), which feed primarily on the termites, particularly during periods of environmental stress (Tongway, Ludwig, and Whitford 1989). Although the interactions between termites and other biota is under-represented in research, ants are known to be important predators in and on the soil and affect virtually all arthropod groups in their realm.

Soil crusts, through their influence on soil surface condition, are thought to enhance conditions for micro- and mesoinvertebrates. Although it is intuitively reasonable to expect increased biodiversity and abundance of soil fauna associated with moss- and lichen-dominant crusts, we are unaware of any data to support this assertion, either from semiarid and arid regions in general or from patterned landscapes in particular. It is generally accepted that grazing of crusts by mesofauna is necessary to mobilize nutrients held up in cyanobacterial filaments and sheaths; however, the significance of grazing and parasitism on soil crust biota is unknown (Metting 1991). Ants may use the crust surface as sites for enhanced seed harvesting, but to date no studies are available to demonstrate this possible interaction.

Roles in Landscape Development

Soil Biota and Development of Landscape Patterning

In many arid and semiarid environments, patterning results from distribution and cycling of water and essential nutrients by local-scale primary and secondary ecological processes (Tongway and Ludwig 1990; Tongway 1991). Because essential moisture and nutrients arrive in pulses, such as after high-intensity rainfall or massive erosion events, long-term stability of these systems is reliant on redistribution and cycling processes. Patchy distribution of resources in arid landscapes leads to the development of nutrient-rich "resource islands" (Garner and Steinberger 1989) or "fertile patches" (Tongway 1990) within which plants and animals are concentrated. This heterogeneity enables a more productive system than one in which resources are uniformly distributed (Tongway and Ludwig 1994). Although the primary processes involved in initiating and maintaining landscape heterogeneity are well understood, inadequate attention has been given to role of secondary biological processes involving the soil biota.

Although the importance of mechanisms affecting soil and ecological processes such as pedoturbation, nitrogen cycling, infiltration, and erosion is widely accepted (see above, Roles of Soil Biota in Ecological Processes), the mechanisms themselves are not adequately described or understood in the light of their potential contribution to the genesis of patterning in banded landscapes.

Several authors have explored the possibility that termites (at least) may have contributed directly to the initiation of landscape patterning. Most allude to the possibility that small-scale effects associated with termites (Macfayden 1950) may, over time, coalesce to form larger-scale landscape features. According to this mechanism, termites may have initially created fertile patches of dense vegetation around the periphery or annular zone of their eroded mounds (Noble, Diggle, and Whitford 1989; Eldridge 1994). Other early work supports this hypothesis. In East Africa, Burtt (1942) noted that shrub thickets were confined to areas where there was an accumulation of soil washed from *Macrotermitinae* mounds. Clos-Arceduc (1956) and White (1971) suggested that termite mounds were responsible for the formation of patterned vegetation in arid zones. They postulated that colonies could die due to climatic stress (e.g., an increase in aridity), leaving the mounds to collapse under the effect of increasing erosion. Eroded soil around termite mounds increases runoff, as demonstrated by Janeau and Valentin (1987), and over time, bare mounds may have coalesced to form more-or-less continuous bands. Downslope, the vegetation may have benefited from increased water availability, and this may have facilitated the establishment of vegetation strips. Alternatively, bare areas may develop around termitaria due to overgrazing or drought. These bare spaces may become large enough to increase runoff downslope to an extent that it may be sufficient to support woody vegetation. Observations by Ouedraogo and Lepage (1997) of the close association between termitaria distribution and patterning invite a more detailed investigation of the interaction between the two and the initiation and maintenance of vegetation patterning in banded landscapes. If the spatial distribution of vegetation bands is linked to termite activity as has been suggested by Clos-Arceduc (1956), then nest abandonment could result in an upslope progression of wooded bands over time.

Although there are no empirical data from patterned landscapes, anecdotal evidence from these areas suggests that microbiotic crusts reduce erosion, enhance soil nutrient status (particularly through nitrogen fixation; West 1990), and increase soil structure and aggregate stability (Greene, Chartres, and Hodgkinson 1990). Crusts function as fertile and stable zones, maintained at equilibrium by biotic and abiotic processes. Their small size (<0.1 mm) means that their greatest contribution to the development of landscape heterogeneity may occur on a small scale. Bryannah (1995) noted that microbiotic crusts may be the only form of living cover present on runoff zones in the semiarid woodlands of eastern Australia, stabilizing them in a way that facilitates their regulation of runoff processes. In this way, their contribution to overall maintenance of landscape heterogeneity may be significant.

Disturbance and Succession

We know of no data specific to the role(s) of soil macroinvertebrates in succession in patterned landscapes. However, termites, ants (Andersen 1993), and microphytic crusts (Metting 1991) play important roles in succession in other landscape types and are themselves characterized by successional phases following disturbance.

Although the response of termites to disturbance and their role in succession is poorly studied, the response and roles of ants has received some attention in Australia. Greenslade (1987) described a clear case of succession in an ant community on reclaimed scalded areas in a semiarid woodland in New South Wales. There, reclamation produced an initial increase in density of specialist species that were able to recolonize the degraded areas. Following this phase, there was an increase in incidence of (unspecialized) opportunists and other colonizing species. Eventually, the community was similar to that found in adjacent (nondegraded) areas. It is noteworthy that although this succession was evident in a relatively brief period of time, Greenslade (1987) suggests that the full sequence may span 50 years or more. Although association does not establish causality, parallel responses in community structure between the soil biota and vegetation communities points to the possible importance of soil biota in reestablishment of landscape patterning following disturbance.

Microphytic crusts are commonly pioneering species in revegetation processes (Bailey, Mazurak, and Rosowski 1973). Disturbance-induced physical soil crusts that reduce infiltration and seedling emergence (Valentin 1995) are often colonized by biological elements, initially cyanobacteria such as *Microcoleus* or *Nostoc*. Increased soil stabilization, organic carbon, and soil nutrients (particularly nitrogen) levels may provide threshold levels necessary for developing vascular plants (Isichei 1990). Surface stabilization by cyanobacterial filaments is necessary before lichens can invade and develop into a crust on the surface. These lichens further enhance the nitrogen status of soils (Rogers and Lange 1971; Rogers 1974), eventually allowing mosses to invade and establish. Depending on the soil and vegetation community, the resulting microphytic crusts may persist or be replaced by a vigorous vascular plant community (Eldridge and Bradstock 1994).

External Factors Affecting Soil Biota

Human Impacts

Recognition of the unique functioning of patterned landscapes suggests that they require careful management (Dunkerley and Brown 1995). Activities such as pastoralism (grazing and the use of fire), road construction, and rangeland reclamation practices need to be undertaken with a comprehensive knowledge of the delicate ecological balances involved. However, investigation of the impact of land uses and possible global effects (e.g., climate change) on the soil biota of patterned landscapes is a nascent science.

Future sustainable management of patterned landscapes must involve incorporation of small-scale ecological information into management strategies (Smallwood 1993) and incorporate the use of bioindicators, which are sensitive to ecosystem status. This approach is challenging because of the larger scales at which resources use is viewed in these environments and the complexities involved in assessment, monitoring, and sustainable use of landscapes dominated by local-scale resource partitioning (Stafford Smith and Pickup 1990). Identification of the importance of soil biota in these systems also reinforces the need to manage proactively for the viability of the soil biota (Williams et al. 1993) and to fully investigate the effects of management practices on soil biota prior to their implementation.

Curry and Good (1992) suggest that "the assumption that invertebrates can eventually recolonise without assistance is probably valid in most cases." However, they also note that "there is considerable scope for intervention to accelerate the establishment of desirable species in most situations." Some examples of proactive intervention already exist among traditional practices. Although little studied, the role of termites is recognized culturally as an important component of some of these agricultural systems. For instance, in northern Burkina Faso, where up to 40% of the area is degraded (Kabore and Valdenaire 1991), farmers practice a traditional technique that encourages termite activity on degraded soils by incorporating organic residues into the soil. Stimulating termite activity by placing plant residue on the surface of degraded soils leads to improved soil structure, increased porosity, enhanced infiltration and soil fertility, and ultimately, greater pasture production. Crops and tree seedlings are then planted into these patches. Similar examples exist for traditional agricultural systems in Niger (J. Rajot, pers. comm.).

Pastoralism and Agriculture

Grazing may, at the coarsest resolution, lead to simplification of the soil faunal community through habitat fragmentation, altered fire regimes, and introduction of exotic plant and animals. Furthermore, soil disturbance and alteration of soil physical and chemical status may occur through compaction, erosion, chemical residues in dung, and the use of herbicides and pesticides.

Overgrazing or indiscriminate timber collections in patterned landscapes leading to reductions in vegetation cover has immediate and long-term effects on the distribution, abundance, and activity of soil fauna, particularly termites and ants. For example, in a patterned mulga woodland, Greene (1992) showed that overgrazing lead to removal of grasses, resulting in homogenization of the landscape and compromising ecosystem stability. In the same landscape, Bryannah (1995) showed that the grazing by sheep halved the relative abundance of ants compared with sites grazed by kangaroos only. She also presented some evidence for a variation in the spatial distribution of particular functional groups of ants in response to the changed environmental conditions resulting from grazing.

Data from the patterned mulga woodlands (Bryannah 1995; M.E. Tozer and D. Eldridge, unpublished data) support the notion that increased grazing intensity leads to reduced cover of microphytic crusts over time. These data, although variable, support evidence from other landscapes that indicates that crusts are susceptible to trampling and cultivation. Purported slow recovery rates (Rogers 1974) may result from changes in soil texture, brought about by loss of fine material through wind and water erosion. Our observations in marginal cropping country in other landscapes in Australia, North America, and North Africa suggest that even a single cultivation leads to the demise of microphytic crusts and that reestablishment once cropping ceases is slow.

Role of Fire

Fire is a regular feature of patterned landscapes in both Africa and Australia. Despite this, we found few data on how fire affects invertebrates or microphytic crusts in these landscapes. Tongway and Hodgkinson (1992) warn that in restoration following fire, stabilization of the soil surface precedes the recovery of chemical fertility, and that early restocking, prior to the recovery of biological cycling, may reverse the gains previously made in stability.

Alteration of vegetation as a result of fire has been shown to have a significant effect on arthropod detritivores in the semiarid tropics of northern Australia (Greenslade and Mott 1983). Evidence from nonpatterned semiarid systems indicates that increasing fire frequency destroys microphytic crusts and their associated polysaccharide gels, depleting the microbial food source and hence their populations (Greene 1992; Tongway and Hodgkinson 1992). Like grazing and trampling, fire leads to a slow recovery in microphytic crusts.

Impact of Climate Change

The effect of climate change on soil biota is poorly studied and can only be speculated on. However, it is reasonable to suppose that any generalized global effects will be amplified in semiarid and arid regions where human use (including increased sedenterisation), sparse vegetation cover, and increased risk of wind and water erosion are greatest (Valentin and Bresson 1992). In a study in Mauritania, decreased rainfall and increased incidence of wind erosion over the past 30 years is believed to be responsible for degradation of the vegetation pattern (Gravier, Riser, and Simon 1994). In some tropical regions where desertification is already advanced, the banded woodlands provide the principal source of fuelwood for cooking, heating, and shelter construction materials. In the dry season, these areas are further stressed by grazing by village herds.

Although we have no data on the effects of climate change on microphytic crusts, they may be influenced by the hypothesized increases in summer rainfall over eastern Australia, as a consequence of the "Greenhouse" effect. This may result in decreased coverage of soil crust lichens at the expense of cyanobacteria and mosses, as hydrated lichen thalli cannot tolerate rainfall at temperatures of approximately 40°C (Rogers 1989). More data are needed before we can determine the effects of global climatic change on soil biota. Feedback mechanisms will undoubtably operate, perhaps reinforcing any degradation experienced as a result of climate change.

Soil Biota as Indicators of Landscape Health

In recent years, the use of species or groups of species as indicators of environmental health has received increasing attention. Ants, in particular, have shown some promise, as they are relatively ubiquitous, functionally important at a number of trophic levels, easy to sample, and relatively sensitive to environmental variables and change rapidly in response to environmental change (Andersen 1990).

In the patterned semiarid woodlands, Bryannah (1995) demonstrated both community sensitivity to disturbance (as a result of sheep and kangaroo grazing) and significant association between major functional groups of ants and key vegetation and soil parameters. She presented evidence for variation in the spatial distribution of particular functional groups across the geomorphic gradient comprising runoff, interception, and runon zones. The strong relationship between the abundance of the 'keystone' ant *Iridomyrex* in the various zones and stocking rate may show promise as an indicator of rangeland degradation. However, this spatial element in community structure and its importance in terms of ecosystem functioning require further investigation.

Microbiotic crusts and their associated microbiota are essential components of soil stability and productivity in semiarid rangelands. In the semiarid woodlands of eastern Australia, Tongway and Smith (1989) developed a system to classify the surface condition of red-earths by using soil surface characteristics including cover and type of soil crust. More recently, Eldridge and Koen (1998) demonstrated that foliose lichens in soil crusts were strongly associated with uneroded surfaces in excellent condition. The majority of lichen and moss taxa, however, showed no close association with surfaces of a particular condition class.

Conclusions

This chapter has examined the roles of soil invertebrates, specifically termites, ants, and microphytic crusts, in the genesis and persistence of patterning in landscapes and the implications of this in terms of management of these landscapes. There is some evidence for the role of termites in the genesis of patterning in landscapes. However, the largest body of work encountered relates to the role of termites and ants in the perpetuation of landscape heterogeneity in patterned landscapes, through their role in ecological processes involving redistribution of scarce water and nutrient resources. More research is needed to fully investigate the involvement of ants and termites in these processes and to assess the impact of management practices such as grazing and the use of fire on these organisms.

This review has identified areas in which our knowledge of soil biota is severely limited. First, a greater knowledge is needed of the role that ants play in the maintenance of patterned vegetation, particularly through their role in seed dispersal and seedling establishment, and their influence on the development of small-scale heterogeneity within the larger framework of landscape patterning. Second, we discussed how termites have both a "positive" influence on landscapes (through increased bioturbation and infiltration) and a "negative" influence (by predisposing fine-textured soils to erosion and, therefore, enhancing runoff). Further experiments are necessary to describe precisely the spatial and temporal nature of these influences and the consequences of them in terms of the functioning of patterned landscapes. The operation of these processes, under the influence of external factors such as management practices and possible global effects, may ultimately have a marked effect on the integrity of patterned landscapes in which termites are the dominant soil faunal group.

Data on microphytic crusts are sparse, with most published work emanating from eastern Australia. The review has highlighted a number of particular areas of research deficiency. To understand microphytic crusts in patterned systems on the African subcontinent, we need to develop systems to characterize crusts, particularly those dominated by cyanobacteria (Malam Issa et al. 1999), at least to the level of morphological groups (Eldridge and Koen 1998). Also, data on the natural rates of regeneration of crusts under both sedentary and nomadic forms of pastoralism are clearly needed. Accordingly, their role(s) in the regulation of infiltration and soil nutrition and as agents in primary stabilization of systems and their sensitivity to various management systems warrants greater attention by researchers and land managers.

Finally, this review has reinforced the notion that soil biota are important components of arid and semiarid patterned landscapes, and consequently, they may be useful as indicators of environmental health. Further work is required to establish the causal nature of the association between the soil biota and other spatially patterned elements in these landscapes and to assess the sensitivity of various functional groups to ecosystem stress. To that end, their association with those processes considered critical to amelioration of degradation and land restoration requires quantitative investigation involving field-based experimentation.

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7. Vegetation Dynamics: Recruitment and Regeneration in Two-Phase Mosaics

Carlos Montaña, Josiane Seghieri, and Antoine Cornet

Introduction

Banded landscapes are characterized by bands of dense perennial vegetation oriented parallel to the contour, separated by bare soil (Figures 1.1, 1.10, 1.12, this volume). They are widely distributed globally and have been studied in arid and semiarid climates of Sahelian Africa and the Middle East (White 1971; Wickens and Collier 1971), South Africa (van der Meulen and Morris 1979), Australia (Mabbutt and Fanning 1987; Tongway and Ludwig 1990), and North America (Cornet et al. 1992). White (1971) defined the common characteristics apparently necessary for the existence of a banded vegetation spatial structure. These characteristics are now well known and include a semiarid climate and rainfall runoff as sheet-flow on gently inclined surfaces (chapter 1, this volume). Commonly, the band and interband zones have a similar soil type and texture but not always. For example, some banded landscapes are located on soils with swell/shrink gilgai patterns and dynamics (Dunkerley and Brown 1995; Macdonald, Melville, and White 1999). The most common vegetation association in the bands is a mixture of grass and shrubs and/or trees (Slatyer 1961; Montaña, López-Portillo, and Mauchamp 1990; Seghieri et al. 1997) but can be dominated by grass (Worral 1959), trees alone (Worral 1960), or chenopod shrubs (Macdonald, Melville, and White 1999).

The origin of banded landscapes has been the subject of much conjecture (White 1971; Greig-Smith 1979). Boaler and Hodge (1964) postulated that bands developed from an initially evenly vegetated surface through gradual degradation due to climatic or soil degradation. White (1971) and Boudet (1972) suggested that they originated from colonization of previously bare zones by concentrating resources upslope of natural obstacles to water movement. Mabbutt and Fanning (1987) and Cornet and associates (1992) proposed that the origin of banded landscapes lies in the geomorphic evolution of planar or very slightly convex or concave landforms so as to favor extensive sheet-flow runoff. All these explanations remain speculative because band initiation has not actually been observed. Modeling band initiation has been a major activity (chapter 9, this volume).

Hypotheses as to the overall functioning of banded landscapes have all been related to surface hydrological processes in which resources mobilized by rainfall runoff from the interband are effectively captured within the band and used by vegetation growing there (White 1970, 1971; Wickens and Collier 1971; Tongway and Ludwig 1990; chapter 5, this volume). This commonly results in denser, more perennial plants in the band than would be predicted from the average annual rainfall without spatial redistribution (Ludwig, Tongway, and Marsden 1994). These processes are dealt with in detail in chapters 4 and 5 of this volume. The underlying hypothesis exemplifies the Noy-Meir (1973) proposition that heterogeneous distribution of water in semiarid landscapes improves overall productivity than if water were evenly spread.

The objectives of this chapter are to discuss vegetation dynamics of banded landscapes in the light of the hydrological functioning of the landscape in terms of (1) the overall landscape vegetation structure, (2) the species composition and temporal dynamics at different locations within the bands, (3) the evidence provided by vegetation in upslope band migration, and (4) the effect of human activities on vegetation and band persistence. The data are drawn from the set of sites where formal vegetation studies have been carried out: Mapimi in Mexico, Banizoumbou in Niger, and Lake Mere in Australia, although smaller studies at other sites have also contributed.

Vegetation Band Structure

Band-Interband Patterns

The vegetation composition and structure of the bands proper are very variable between global locations (Table 7.1). White (1971) suggested three types of vegetation bands: those composed basically of grasses, those containing a mixture of grass and shrubs, and those composed of shrubs and trees. The wide range in lifeform suggests that there is an equivalent range in the availability of soil moisture over time and three-dimensional space in the soil. Different soil moisture regimes are caused by differences in the interaction of how much rain falls and its spatial redistribution. Theoretically, less frequent but deeply penetrating soil water additions might advantage trees, whereas grasses might be favored by frequent smaller showers.

Vegetation cover on the interbands was so low at all sites that its dynamics have been largely ignored in the literature. At the Lake Mere site in Australia,vegetative

Table 7.1. Common Aspects of the Vegetation Structure in Several Sites of Banded Vegetation

	Niger site	Burkina Faso site	Mexico site	Australia site
Dominant in thicket core, backbone of the banded pattern	*Combretum micranthum* (shrub)	*Combretum micranthum* (shrub)	*Hilaria mutica* (perennial grass)	*Acacia aneura* (tree)
Dominant upslope the thicket core	*Guiera senegalensis* (shrub)	*Tall annual community* (mainly grasses)	*Flourensia cernua* (shrub)	*Thyridolepis mitchelliana* (perennial grass)
Distributed independently from the banded pattern	—	*Pterocarpus lucens* (shrub)	*Prosopis glandulosa* (shrub)	*Eragrostis eriopoda* (perennial grass)

cover on the interband was never more than 10%, whereas the mulga band exceeded 50% foliar cover and the upslope grassy fringe or ecotone had 25% cover (Tongway and Ludwig 1990).

In the Sahel, Couteron, Mahamane, and Ouedraogo (1996) and Couteron, and co-workers (2000) studied the differences in band structures at sites at Banizoumbou (Niger) and Bidi (Burkina Faso) by examining the distribution of woody species. The rainfall distribution is similar, and the dominant species at both sites is *Combretum micranthum*. The soil texture at Bidi is sandier and lacks the cemented ironstone gravel present at Banizoumbou, so that the infiltration rates are higher and the soil water more evenly distributed across the landscape. As a consequence, the vegetation banding, as assessed by measuring the density of juveniles of *C. micranthum* across the vegetation band at Bidi, is not as strongly differentiated as at Banizoumbou and has a lower overall biomass per unit area. These vegetation data illustrate variations in intrinsic banded landscape runoff/runon processes (function).

Within-Band Patterns

The vegetated bands can be divided into three basic sections (Figure 7.1): (1) the upslope fringe, (2) the main body of the band, and (3) the downslope fringe (Cornet et al. 1992; Montaña 1992; Couteron et al. 2000). One would expect the upslope fringe to receive a higher frequency of runon events and more water overall than the downslope fringe, which would receive only ambient rain plus rare runon from exceptional events. This expectation is supported by vegetation data.

For example, at Lake Mere, the upslope fringe was composed of perennial grass cover of 20.2% that is composed of nine species and a two-species shrub cover of 7.4%. The main body of the band comprised 12.4% perennial grass cover that is

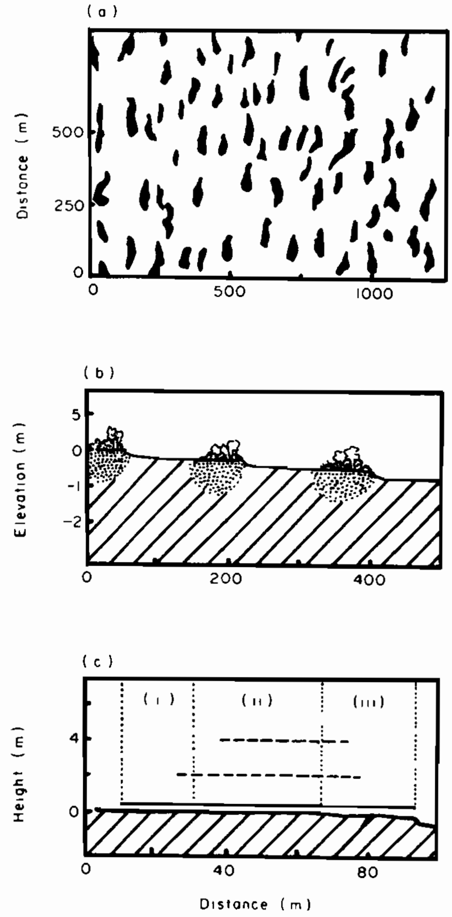

Figure 7.1. Schematic representation of banded vegetation patterns from the southern Chihuahuan Desert (Mexico). (a) Aerial view at 1:25,000 scale showing the vegetation bands (in black) surrounded by almost bare areas. (b) Idealized cross-section of the landscape showing the distribution of vegetation and soil water moisture after rain (dotted areas in the soil profile). (c) Idealized cross-section of a vegetated band. Horizontal straight lines indicate the range vegetated and the height of herbaceous species (continuous line), shrubs (lower dashed line), and small trees (upper dashed line). Dotted vertical lines indicate the three subdivisions of the bands used in this work: (i) upslope, (ii) main body, and (iii) downslope. (Modified from Fig. 1, Montaña 1992.) Permission courtesy of Blackwell Science Ltd.

composed of nine species and 40.1% shrub/tree cover composed of two species. There was no downslope fringe (Tongway and Ludwig 1990), implying that resource availability there was too low to support plant populations. This accords with the comparative hydrological analysis in chapter 5 of this volume.

At Mapimi, a greater number and diversity of species were found on the upslope fringe compared with downslope (Figure 7.2). The upslope fringe had much higher species richness (5.43 ± 0.51; range, one to 18 species) than the downslope fringe of the vegetation band (1.72 ± 0.12; range, zero to four) as measured in 2 × 1-m quadrats (Montaña 1992). Seedlings growing in full sunlight grew larger than those in shade. There was a distinct senescence zone on the downslope side of the band.

There is a diversity of germination strategies among the commonly found plant species. Some plants germinate in multiple locations, whereas others appear to

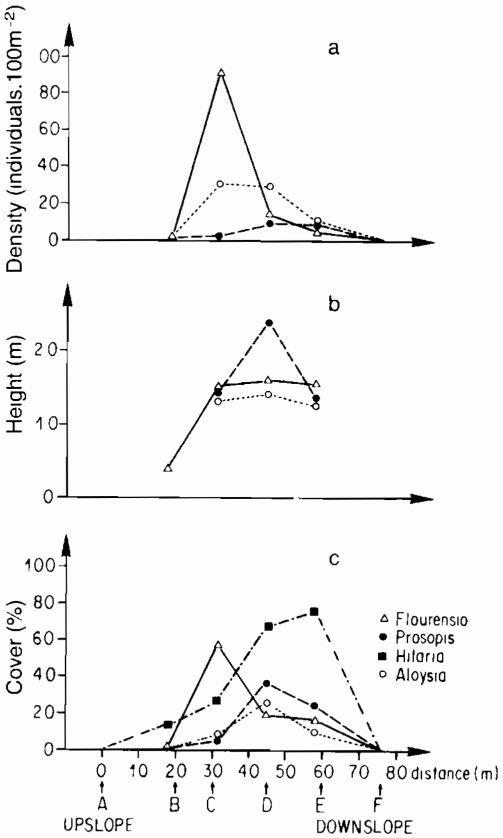

Figure 7.2. Density (a), height (b), and cover (c) of the most abundant shrubs and small trees in a vegetation band from the southern Chihuahuan Desert (Mexico). (Modified from Fig. 16.6, from Cornet et al 1992.) Permission courtesy of Blackwell Science Ltd.

favor a restricted set. For example, in Mexico, *Prosopis glandulosa* seedlings were recorded both in the band and in the bare area, whereas *Flourensia cernua* seedlings were dominantly found in the upslope fringe (Montaña, López-Portillo, and Mauchamp 1990; Mauchamp et al. 1993). In Niger, 50% of *C. micranthum* seedlings were in the core, and similar proportions of the remainder were in the upslope and downslope fringes, whereas *Guiera senegalensis* specialized in either core or upslope fringe sites (93%) and only 7% in the downslope fringe (Couteron, Mahamane, and Ouedraogo 1996; Couteron et al. 2000). These observations are consistent with the notion that the future floristic composition (and hence the vegetation structure), at a specific site, are mainly influenced by the availability of safe sites and the ability of seeds to reach them (Harper et al. 1961; Harper, Williams, and Sagar 1965; Harper 1977) and also by the biotic and abiotic conditions for plant establishment (Grubb 1977).

Vegetation Band Dynamics

A greater part of published vegetation studies in banded landscapes has been concerned with the dynamics of the vegetated bands, mainly in the upslope fringe or ecotone, where the dynamics are greatest. Indeed, the dynamics of the long-lived vegetation in the core of the band have had little attention due to the long timeframe needed to study these organisms effectively (Tongway and Ludwig 1990; Montaña 1992; Galle, Seghieri and Mounkaila 1997). For example, Mulga (*Acacia aneura*) is believed to live for about 250 years (Crisp 1978), implying that successful establishment of new plants need not be a frequent event. The vegetation dynamics studies were mainly undertaken to investigate the basic processes of colonization and plant species succession and to provide information about possible upslope migration processes. These studies accepted the controlling influence of runoff/runon hydrological processes in principle but looked in finer detail at the consequences for vegetation.

Plant Dynamics in Response to Available Moisture

Herbaceous Plants

At the scale of the band upslope fringe, soil moisture dynamics influence both germination and establishment of herbaceous plants (Cornet et al 1992; Montaña 1992); over time, the species composition implies successional development. This pattern is characterized by the presence of annual or ephemeral plants at the extreme upslope edge of the ecotone followed in a downslope sequence: short-lived perennials and then long-lived perennials more closely resembling the species composition of the core of the band. For example, at Mapimi, between 1982 and 1986 in the upslope fringe there was a decrease of herbaceous perennials (forbs) and an increase of both perennial grasses and saplings of woody species (Cornet et al.1992). Further, Montaña (1992), studying the spatial distribution of plants along a transect from the upslope edge of the fringe to the main body, found (1) a gradual increase in species richness up to a peak and then a decrease (as would be expected within an ecotone), (2) changes in both the lifeform and the floristic dominance spatially matched this peak, and (3) a change in the distribution of species abundance from geometrical to log-normal, as would be expected in a successional process (May 1981).

Woody Plants

The above findings for herbaceous vegetation do not extend to woody plants, where the age distribution of *P. glandulosa*, a long-lived woody plant was used to seek evidence for progressive upslope migration (López-Portillo and Montaña 1999). The hypothesis underlying this study was that if upslope migration were a continuous process, both the age and size classes of *P. glandulosa* would increase systematically downslope within a band. An inventory of plants showed this not to be true. In particular, younger plants were not more abundant in the upslope locations, and larger individuals were not found in downslope locations within the bands. Some *P. glandulosa* close to the upslope edge appeared to be greater than 50 years old. However, dead trees in the contiguous bare areas up and down slope of the band suggest that some sections of the downslope part of the bands have contracted, the rest of the population remaining stable (López-Portillo and Montaña 1999). *P. glandulosa* is known to have a strong invasive propensity (Brown and Archer 1990), particularly into landscapes where grass competition has been reduced by grazing (Bush and van Auken 1990). Its seeds are dispersed widely by large herbivores, so it may be a poor indicator for the upslope migration of "natural" bands.

Seed Dispersal

There appear to be no specific studies of seed production as such in banded landscapes. The few studies made on seeds relate to dispersal and indicate that the seed bank is patchily distributed and concentrated mainly in the vegetated patches. Mauchamp and associates (1993) showed that 90% of seeds were beneath the crown of adult plants in the surface soil layer for the shrub *F. cernua*, the dominant vegetation cover on the upslope edge of bands in Mexico. Montaña, López-Portillo, and Mauchamp (1990) recorded most *F. cernua* seedlings less than 3 m away from the nearest adult and not any more than 5 m distant. Moreover, conditions for *F. cernua* recruitment are met only in the upslope ecotone between the main body of the band and the bare area (i.e., in the colonization front). These characteristics of *F. cernua* recruitment, coupled with the observation that some bands have a dense grass cover upslope of the *F. cernua* populations, led Mauchamp and associates (1993) to the conclusion that *F. cernua* populations persist in vegetation bands by metapopulational dynamics involving successive colonizations and local extinctions (Pulliam 1988). This is consistent with conventional seed dispersal and establishment observations: primary and secondary dispersal and seed density decrease with distance from the source plant (Harper 1977; Nelson and Chew 1977; Schaal 1980; Howe and Smallwood 1982; Boyd and Brum 1983; Green 1983; Chambers and MacMahon 1994).

The vegetation bands have microtopographic features that favor seed accumulation. Reichman (1984) and Ellner and Shmida (1981) showed that seed trapping in natural and artificial depressions in the soil surface is common in arid lands generally. In desert ecosystems, Chambers and MacMahon (1994) stated that few long-lived perennials have persistent seed banks, whereas annual species range from high to transient (Kemp 1989). In banded landscapes, seed may be washed or blown by wind across the bare interband zone and accumulated by the vegetation band. Seghieri and colleagues (1997) found a 180-fold difference between the annual soil seed bank at the core of the band compared with the bare area. The transport of seeds between vegetation bands, by runoff water or wind, may be a source of regeneration in degraded bands (Mauchamp et al. 1993). They found that *F. cernua* seedlings germinated all over the band after rain, strongly suggesting redistribution and concentration of seeds in the band by sheet-flow.

As mentioned above, domestic and wild animals may also disperse seeds, as in the case of *P. glandulosa*, as the distribution of seedlings was clumped in animal camps. This manner of dispersion might increase the probability of seed survival in the landscape as a whole because of the high predation of seeds by insect larvae close to parent plants (Montaña, López-Portillo, and Mauchamp 1990). *P. lucens* in Burkina Faso may also have dispersal mechanisms not related to the runoff/runon banded landscape processes (Couteron et al. 2000).

Upslope Band Migration

The notion of upslope migration or movement of the vegetation bands has been a common thread in all studies of banded landscapes (White 1971; Greig-Smith 1979; Mabbutt and Fanning 1987; Montaña, López-Portillo, and Mauchamp 1990; Tongway and Ludwig 1990; Montaña 1992). Most of the evidence for the movement of whole bands is circumstantial and collected over short time spans relative to the functioning of the landscape. In particular, observations of dead trees just downslope of the band provided strong prima facie evidence of band movement. When linked with the accepted runoff/runon processes for band-interband pattern maintenance, these plant observations provide a hypothesis worthy of testing. Upslope migration of vegetation bands has been extensively modeled (chapters 8 and 9, this volume), and several plausible scenarios exist.

There is a little evidence of the upslope migration of whole bands, but it is not compelling in a global sense. In Mexico, the edge of the band moved 4 m upslope between 1982 and 1987 and thereafter remained static. Upslope retraction of the vegetation in the downslope fringe did not commence until 1988 (Montaña 1992). This suggests that any upslope movement of the band as a whole is not a steady whole-of-band migration. There may be a time lag of a number of years between upslope edge advance and the downslope edge retraction, depending on seasonal conditions. These spatial dynamics of species succession also reflect the gradual development of appropriate edaphic habitat in the upslope fringe. In Niger, large tree roots found in the interband zone (J. Rajot, pers. comm.) imply that trees once occupied this zone.

The relative dearth of actual measurements of genuine upslope migration, as opposed to periodic expansion/contraction of either the upslope or downslope fringe in response to alternating weather regimes, implies that the process is probably intermittent rather than continuous. The evidence also suggests asynchronous movement of the respective edges (Montaña 1992). Measuring a rate of migration has therefore not been fruitful. Perhaps a study of long-term climatic variation would be able to shed more understanding on the dynamics of band migration in that there could be periods when migration was active and rapid and a time when it was quiescent. In some systems, soil biogeochemical processes are implicated in the form of siliceous hardpan formation (Mabbutt and Fanning 1987), implying near-geologic time spans in any movement of the vegetated bands. There are no observations on banded landscapes over the century time scales that can be used to confirm or refute the basic notion.

Degradation of Vegetation Bands due to Human Activities

Most research on banded landscapes has been concerned with the basic nature of their functioning, and the application of this knowledge to examining the effects of stress and disturbance on managed banded landscapes is essential. At Lake Mere, a range of grazing pressures was experimentally applied to a site where the band comprised a perennial grassland ecotone and a mulga woodland (Anderson and Hodgkinson 1997). They found that the perennial grass sward that dominated the ground layer of the ecotone served an important functional role in that the grass slowed and obstructed the flow of runoff water from the interband (Tongway and Ludwig 1997), capturing a greater proportion of runoff compared with a treatment in which domestic and wild herbivores had consumed the greater part of the grass, permitting runoff water to run through the band. As a consequence, both the grass and the mulga were moisture-deficient, as shown by predawn water potential measurements, threatening their survival (Anderson and Hodgkinson 1997). This is a clear example of the role of perennial vegetation in directly contributing to landscape function. Without this resource-capturing process, the existence of mulga banding would be threatened, as the banded mulga landscapes are intrinsically less resource capturing than either the Mexico or Niger banded landscapes (chapter 5, this volume).

Wu and associates (2000) found similar effects of degradation to the Australian work. Their retrospective remote-sensing study in Niger showed that between 1960 and 1992, the bands near Hamdallaye (13° 34' N, 2° 35' E) became seriously fragmented due to human activity (Figure 1.8, this volume). The period of the photographic review coincides with a massive build-up of stock numbers (Cisse 1981). Firewood harvesting also increased over this period, with tracks being made to both collect and transport the wood. Fragmentation took several forms. The bands broke up into shorter sections, permitting runoff water to bypass the band and become lost from the system. Wu suggested that lacunarity analysis is an appropriate tool to quantify this process. In addition, the downslope boundary of the bands retracted upslope over the period, also indicating that the water relations in the downslope fringe of the band had been adversely affected. López-Portillo and Montaña (1999) also recognize overgrazing as a vector of change in band functioning.

The consequences for management are clear. Increasing human pressure limits plant establishment everywhere, but the least favorable sites are more adversely affected (e.g., the downslope fringe). The effect of human pressure is to restrict or limit the capture of resources by the bands. Water, topsoil, litter, and seeds flow around or through degraded bands and out of the system, so that resource capture by less favored sites is even more restricted (Ludwig et al. 1997). These stresses might favor upslope expansion of some band fragments in the short term but would accelerate the disorganization of the banded system as a whole in the long term (Wu, Thurow, and Whisenant 2000). Adequate monitoring of band integrity needs to be implemented with the explicit intention of providing early warning signs of system degradation, together with clear guidelines as to appropriate ways to manage the landscape.

Summary

Noy-Meir (1979/80) discussed the biology of desert vegetation in terms of two competing hypotheses that he named *autecological* and *ecosystem.* The former hypothesis suggests that "the dynamics of each population are determined by its independent reaction to the environment," whereas the latter holds "that nature, in general, consists of integrated ecosystems, in which all populations and many environmental factors are (directly or indirectly) linked and regulated by biological interactions and feedbacks."

Clearly, the complex interrelationships between vegetation and various parts of the physical environment described in this review support the dominance of the ecosystem hypothesis. Explicit integration and cross-linking of knowledge about biota, resources, and physical conditions is essential to understand banded vegetation function (chapter 2, this volume). A range of abiotic processes (Shmida, Evenari, and Noy-Meir 1985) as well as biotic processes (Niering, Whittaker, and Lowe 1963; Noy-Meir 1985; Callaway 1995) contributes to the structure and functioning of banded landscapes. Also, spatial and temporal variability in the development of the successional process (Yarranton and Morrison 1974; Robinson et al. 1992), in turn, may arise from the variability in the outcome of biological interactions (Bronstein 1994).

Banded vegetation patterns can be considered as a nested organizational hierarchy (Urban, O'Neill and Shugart 1987; Mauchamp 1992). At the coarsest or landscape organization level, banded landscapes are a mosaic composed of vegetation bands and bare areas, linked by the dynamic redistribution of rainwater by sheetflow into an alternating runoff/runon pattern. At a second finer-scale level, as soil water availability increases from the upslope edge to somewhere within the vegetation band, the vegetation cover and biomass increases to a maximum (Galle, Ehrmann, and Peugeot 1999) and then decreases to the downslope bare zone. If the availability of light changes in concert with the gradient in water and biomass, zonation of vegetation species composition may occur, as it does in Niger. Without light restriction, only the plant population size distribution is affected, as in Mexico and Australia. Few of the models have explicitly incorporated the effects of biological interactions between vegetation elements at the within-band level (Mauchamp, Rambal, and Lepart 1994; Thiéry, d'Herbès, and Valentin 1995; Dunkerley 1997a,b; Lejeune, Couteron, and Lefever 1999).

A third and least-studied level considers the individual plants within the vegetation array. The elements linking them are demographic processes, biotic interactions (e.g., facilitation and inhibition/competition), and fine-scale abiotic factors, (e.g., microtopography, soil crusts). The present review reveals that vegetation dynamics are the outcome of complex interactions at this level. Models predicting the behavior of individual system elements at this scale are inevitably complex, and none yet exist. The outcomes may be analyzed in terms of both succession models and of more process-based conceptual frameworks involving feedback loops (chapter 2, this volume). In the future, manipulative experiments in natural communities and careful analysis techniques (Gurevitch and Collins 1994) will be essential to verify those models.

Demographic processes such as dispersal and establishment need much more elucidation to build on the work of Mauchamp and co-workers (1993), López-Portillo, Montaña, and Ezcurra (1996), and López-Portillo and Montaña (1999). This becomes important as human-use patterns become threatening processes to the survival of the vegetation system. The differential survival of mature plants in the different zones of the pattern implies spatially linked physiological limitations for perennial species in relation to water availability and other factors. These relationships need further attention to shed light on the functional role of the observed vegetation structures in the provision of ecosystem services (Mauchamp et al. 1993; Montaña, Cavagnaro, and Briones 1995; Seghieri and Galle 1999).

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8. Multiscale Modeling of Vegetation Bands

Andre Mauchamp, Serge Rambal, John A. Ludwig,
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Introduction

The questions of Watt (1947) ("How are the individuals and the species put together? What determines their relative proportions and their spatial and temporal relations to each other?") can be answered by examining flows and budgets of energy and matter at the scale of a specific vegetation band or their spatial relationships and aggregation. Both questions correspond to the objectives that Wiens (1984) gives to community ecology: "to detect the patterns of natural systems, to explain them by discerning the causal processes that underlie them and to generalise these explanations as far as possible." Those patterns and processes determine the functioning of ecosystems and population dynamics that are closely linked by similar underlying spatial processes.

Systems organized in space have common traits that play an important role in ecosystem functioning and population dynamics: the existence of ecotones (Wiens, Crawford, and Gosz 1985; Hansen and Di Castri 1992), the importance of horizontal flows (Peterjohn and Correll 1984; Kareiva 1985), equilibrium and/or stability scale dependence (De Angelis and Waterhouse 1987), links between variations in time and space (Delcourt, Delcourt, and Webb 1983; Solbreck and Sillen-Tullberg 1986; Wiens et al. 1986), and feedbacks between processes at different scales (Archer 1990; Schlesinger et al. 1990). Watt (1947) underlines, in such systems, the relationship between time dynamics and spatial patterning. In each case, two time and spatial scales are important to recognize: (1) that of the entire system, heterogeneous and stable as a whole, and (2) the band, more homogeneous, smaller and having a short life span. Local changes within a band are linked to neighboring patches, and spatial heterogeneity is a structure influencing local processes. This dual spatial and temporal approach has been widely used (Moloney et al. 1992).

Today's landscape analysis techniques span a broader range of scales than the two levels used by Watt (1947) and *imply the development of a body of theories for between-scale relationships.* Defending a hierarchical approach of landscape ecology, Urban, O'Neill, and Shugart (1987) underline the interest of combining hierarchies of functional levels. At each level, internal forces responsible for changes over time are identified, and links are established with and between biotic and abiotic mechanisms at both smaller and larger scales. This approach better integrates the impact of disturbances (Pickett et al. 1989), to link a possible equilibrium at one level to nonequilibrium at another level and to evaluate human impacts at the correct scales in both space and time. The efficiency of the hierarchical approach depends on the ability to describe the system under study as a combination of well-defined units of different scales (Peterjohn and Correll 1984). The difficulties increase with poorly defined limits, gradients, or continua (Greig-Smith 1983; Wierenga et al. 1987; Turner et al. 1991).

In such a context, banded patterns or *brousse tigrèe* is a spatially complex system with sharp limits that depend mainly on a single limiting physical factor, water availability. It can be studied and modeled across at least four spatial scales: the band, the ecosystem, the hillslope, and the whole landscape. Sharp limits between components at each scale make the hierarchical model straight-forward to establish. The dynamics in time and space are due to processes taking place at all four scales, as underlined by the studies on banded landscape functioning and long-term evolution (Hemming 1965; Cornet, Delhoume, and Montaña 1988; Mabbutt and Fanning 1987; Montaña 1992; Mauchamp et al. 1993). Both models presented in this chapter explicitly consider the spatial structure of the landscape and address the consequences of this structure on the functioning and resistance to disturbance of the system.

Band-to-Ecosystem Model

An overtly spatial simulation model was developed to combine processes determining vegetation dynamics and mechanisms that affect ecosystem-scale flows of energy and matter. The chosen scale was that of two interlinked bands, one acting as a source and the other as a sink for water. Our purpose was to model the influence of a variable spatial context on the interactions between flow, ecosystem function, and plant population dynamics. The model is both spatial and mechanistic. Space is explicitly taken into account by simulating the changes in soil water status and vegetation cover in each quadrat of a transect and the relationship between two adjacent quadrats (surface water flow and seed dispersal). Individual species occupy unique spatial positions and compete for water and solar radiation resources within the same quadrat. It is considered that the only interaction between quadrats is surface water flow and that the plants do not extract resources from neighboring quadrats. The model makes dynamic forecasts of plant populations by predicting dispersal, germination, growth, survivorship, and reproduction by using simple submodels and was used to determine whether the functional processes represented contain sufficient realism to capture the pertinent features of the system.

Design and Structure of the Landscape Model: Banded Landscapes in the Chihuahuan Desert

The example underlying this model is the "mogote" from the Chihuahuan Desert in the Mapimi Biosphere Reserve (Mexico, 26°N latitude, 103°W longitude). Mean annual rainfall is 284 mm concentrated in summer, more than 70% occurring from June to September. The banded landscapes cover more than 30% of the area of the reserve, and 25% of the banded landscape is composed of dense bands. The parameters used in the simulations are derived from the literature or previous studies on Mexican banded landscapes (Montaña 1992; Mauchamp et al. 1993). The main plant species are a perennial C_4 grass *Hilaria mutica* Buckl. Benth. (tobosa grass; Hm), a shrub *Flourensia cernua* DC (tarbush; Fc), and a tree *Prosopis glandulosa* var. *torreyana* Torr. (honey mesquite), both of the latter being C_3 plants. These three species and an associated assemblage of annuals with low biomass largely dominate the vegetation cover. Climatic data from 1979 to 1991 came from the meteorological station on the reserve. This sequence was used to generate 50 years of climatic variation for use in a simulation. The initial 13 years follow the observed sequence, and the next 37 were selected at random from the observed sequence. Simulations were initialized with a specified level of plant cover and a ratio of 150 m of bare soil to 50 m of vegetated band (3:1), corresponding to the average of several field observations.

Patch-Interband Model

The model has been described in detail by Mauchamp, Rambal, and Lepart (1994), and only the main processes involved are discussed here. The model is based on three assumptions:

1. Water and solar radiation are the overriding factors limiting primary production. The availability of water is calculated with a daily time-step and varies spatially. The rate of infiltration and the existence of surface water flow in a single direction determine it. The availability of solar radiation is determined by extinction within overlying vegetation layers.
2. All stages in the life cycle of the plants are related to the availability of water and to their carbon budget. The carbon budget is calculated with a time-step of 20 days.
3. Two types of interindividual interactions are simulated: the simultaneous use of the same soil water with no hierarchy between species, and the extinction of solar radiation with a hierarchy depending on height (see Table 8.1 for a summary of model processes, species grouping, and time scales).

The unidirectional orientation of vegetation bands allows the area to be modeled by using a transect perpendicular to the vegetation band in the direction of the greatest slope. The vegetation and water balance were simulated at the scale of 1 × 1-m quadrats. The vegetation cover on each quadrat was divided into 12 classes: one class of annuals and three classes of perennials species (grasses, shrubs, and trees) times three age classes. Its total biomass and percentage of ground shaded or covered further described plant cover. The soil water status across the transect was simulated to a depth of 2 m with 10-cm layers. Each cell of 1 m^2 × 10 cm was characterized by its water content and water potential. A multilayered bucket model with a daily time-step simulated changes in soil water content.

The low water permeability of the soil surface in bare areas and the slight slope can result in substantial volumes of runoff. The USDA Soil Conservation Service method (Boughton 1989) was used to simulate runoff and infiltration. The water input on each quadrat was the sum of the daily rainfall and the incoming surface flow from upslope quadrats. Evapotranspiration was composed of the evaporation from the bare soil and the plant transpiration as a function of plant cover. Evaporation was controlled by the water content of the top 20 cm of soil and extracted from the soil profile according to an exponential extinction function. Transpiration was calculated for each class of plant cover. Plants extracted soil water following Feddes, Kowalik, and Zaradny (1978) within the same quadrat (see limit of this assumption for desert plants in Manning and Barbour [1988] and in Briones, Montaña, and Ezcurra [1996]).

The carbon source was net photosynthesis, and the sinks included respiratory costs for maintenance and senescence. For any given species, its cover, and therefore its evaporative surface, increased with increasing biomass only if the cumulated cover within the corresponding layer was lower than 100%. Competition for space was simulated by using an interspecific dominance hierarchy. A decrease in live biomass occurs when maintenance costs are higher than assimilation. The detachment of the standing dead biomass of perennial grasses follows an S-shaped curve with increasing daily rainfall.

Yearly seed production was generated from mature individuals depending on the carbon budget of the previous year, and seeds were dispersed around adult plants according to a normal distribution. Ten percent of the seed rain was randomly distributed to take into account dispersal by animals and surface runoff. Germination commenced from a set date controlled by air temperature and soil water content. Seedlings were subjected to random mortality and growth according to their carbon balance. The probability of individual death was related to the number of days with negative carbon budget without age limits.

Model Simulation Runs: Spatial Segregation of Plant Species

The use of field observations as the initial conditions caused the model to develop dense cover over the entire band, and contraction was limited to the last downslope meters. The higher survival of mature plants and seedlings of Hm on the downslope side of the band was related to a slower increase in cover: after 10 years, the sum

Table 8.1. Summary of Processes, Species Grouping, and Time Scales for the Band Model

Grouping	
Functional group	Dominant species
Annual species	
Perennial grasses	Tobosa grass
Shrubs	Tarbush
Trees	Honey mesquite

Time scales	
Process	Time Scale
Infiltration, redistribution	1 day
Root water uptake, transpiration	2 days
Carbon budget, growth	20 days
Seed production, dispersion	1 year
Germination, survival	Variable
Seedling stage	<1 year
Juvenile stage	<5 years
Infiltrability	1 year

Processes		
Soil water budget	Infiltration	USDA Soil Conservation Service
	Redistribution	Field capacity bucket model
	Evaporation from bare soil	Ritchie (1972) + exponential extinction
	Transpiration	Cover-dependent maximal transpiration
	Root water uptake	Feddes et al. (1978)
Plant carbon budget	Photosynthesis	WUE-based, cover- and temperature-dependent
	Maintenance respiration	$Q_{10} = 2$–dependent
	Growth pattern	Biomass-cover relationship
Population dynamic	Seed production	Annual carbon budget-dependent for mature individual
	Seed dispersal	Gaussian distribution + white noise
	Seed bank	No
	Germination	Water potential-dependent + random mortality
	Survival	Carbon budget-dependent
Canopy structure		
	Layer 3	Trees
	Layer 2	Juvenile trees + mature shrubs
	Layer 1	Perennial grasses + juvenile shrubs
	Soil surface	Seedlings

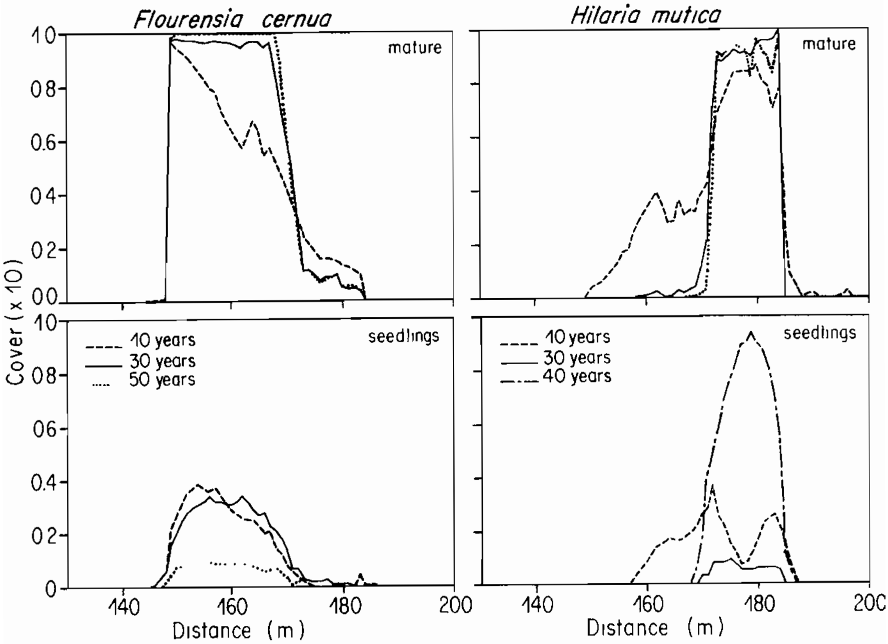

Figure 8.1. Simulation of the changes in both mature and seedling vegetation cover for a stripe composed of two species, the C_4 grass *Hilaria mutica* and the shrub *Flourensia cernua*. The model was run for 50 years with the initial vegetation cover set to those observed in the field. For Hm, the seedling cover after 40 years is displayed to show its large variation over time.

of the cover of the two species did not exceed 70% between 165 and 175 m (Figure 8.1). The dominance of Fc at the upslope edge and that of Hm at the downslope edge became more pronounced after 30 years. The C_4 grass was almost completely excluded under the shrub layer. This was due to the extinction of the photosynthetically active radiation under the plant cover and to the greater sensitivity of Hm to low irradiation (Cunningham, Balding, and Syvertsen 1974; Nobel 1980). A dense cover of grass can therefore only maintain itself in a downslope position, where there are gaps in the shrub cover. Such gaps, which were not present in the initial model conditions and representing an average of several transects, are actually found in the field resulting from local disturbance or mortality. The development of shrub cover depended almost entirely on functional parameters of the shrub itself and was relatively independent of the presence of grass cover.

Seeds were present throughout the band in quantities that increased for both species in proportion to its cover. Germination was complete under cover because of the reduction of direct evaporation but showed large interannual variations (e.g., Hm 40 years). No germination occurred in totally bare areas. Seedling survival was strongly affected by lack of solar radiation throughout most of the band when under cover, with no seedling surviving beyond a year. During the 50 years of simulation, recruitment was only recorded in the upslope few meters of the band, which is in good agreement with field observations.

The dynamics of vegetation cover during the simulations suggest that the initial conditions have an important effect on the model output. They show that differences in the functional parameters of each species (water-use efficiency and sensitivity to solar radiation extinction) influence the dynamics of the shrub/grass zonation. This zonation is related to the disappearance of the grass under the cover of shrubs. The capacity of the grass to maintain itself in the absence of the shrubs suggests that bands of grass might survive within the shrub cover or that bands might consist entirely of grass; both of which are observed in the field. The recruitment of Fc occurring on the upslope side of the band shows that the upslope movement of bands could be simulated. The simulations showed that despite the simplifications (time-steps, linearity of many processes) and the hypotheses selected (water and solar radiation as the only limiting factors, carbon budget dependence of survival and reproductive effort), the model was able to adequately describe the dynamics of the system.

Ecosystem-Level Predictions of Water Budget Under Current Climatic Conditions

Water budgets were calculated for 13-year simulations by using the actual rainfall data from Mapimi. At the scale of a system incorporating a bare area and a vegetation band, the simulated transect was open downslope, and water left the system as runoff. If no vegetated band was present and the whole transect consisted of bare soil, more than 55% of the water entering the transect would be lost as surface runoff. This quantity was reduced to 25% when a 50-m-wide vegetation band was present. On a daily basis, runoff expressed as a percentage of the total rainfall over the transect, varied as a sigmoidal function of rainfall. No runoff occurred if daily rainfall was less than 10 mm; it increased and then stabilized at 80% for daily rainfall greater than 45 mm. At the scale of a 1 × 1-m quadrat, the annual soil water budgets provided a test of the continuity equation (inputs = outputs). On average, little change was recorded in the soil water storage between the start and the end of the year at any position within the band. The components of these budgets are shown in Figure 8.2. The actual evapotranspiration (AET) over the simulation period was approximately equal to infiltration. AET was much lower than annual rainfall in areas bare of plant cover with low water infiltration. AET reached 300% of total rainfall in areas of dense vegetation cover, where runoff was restricted. In Figure 8.2, AET was 52% of rainfall in bare areas and 283% at the upper edge of the band, which agree with the values of 60% and 287% given by Cornet and co-workers (1992) for comparable landscape positions. AET decreased downslope and was 137% at the downslope edge of the band where runon occurred less frequently.

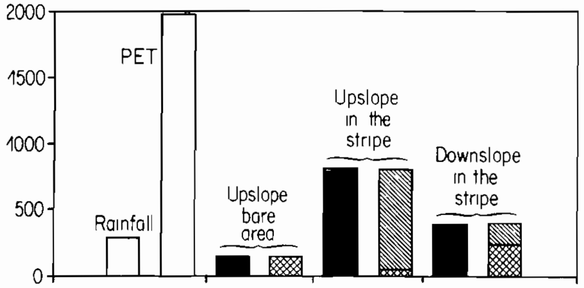

Figure 8.2. Annual soil water budgets, millimeters of H_2O, in three positions along the transect (averages for a 13-year simulation). Empty bars represent the climatic inputs: rainfall amount and potential evapotranspiration. The infiltration (filled bars) is, on average, equal to the actual evapotranspiration (hatched bars represent transpiration and cross-hatched bars soil evaporation).

The simulations show that the bare zone is not closed, because runoff downslope toward the next band was predicted. The total water budget underlines the importance of the effect of concentrating water, the vegetation in the band receiving 200 to 300% that of rainfall. These results are confirmed by field results (Cornet et al. 1992).

Effects of Climatic Change

Global change models are powerful tools for the study of climates and climate changes. The model UKTR of the Hadley Centre for Climate Prediction and Research of the U.K. Meteorological Office is a fully coupled atmosphere-deep ocean model that allows more realistic simulation of ocean–atmosphere interactions. The model has an interactive representation of the land surface and sea-ice, and its horizontal spatial resolution is 2.5° longitude × 3.75° latitude. To explore the effects of a gradual increase of CO_2, two integrations, each of 75 model-years, were carried out: a control run and a perturbed run. In the perturbed run, the greenhouse gas concentration was increased by 1%, compounding annually, which is close to the IPCC Business-as-Usual emission scenario, that results in a CO_2 doubling in about 70 years. Our simulation allows for the fact that concentrations of atmospheric CO_2 do not change abruptly. For mesoscale analysis, the output data stored were relative to both our control and perturbed runs. Depending on the climate variables involved, either daily or monthly time series were stored. In this section, we used results limited to only one UKTR grid cell, which included the Mapimi Reserve and annual rainfall. For this grid cell, the control annual rainfall was 275 ± 80 mm, a surprisingly close value of the observed 284 ± 65 mm for the period 1979 to 1991. We analyzed the linear trends of the deviation between the perturbed

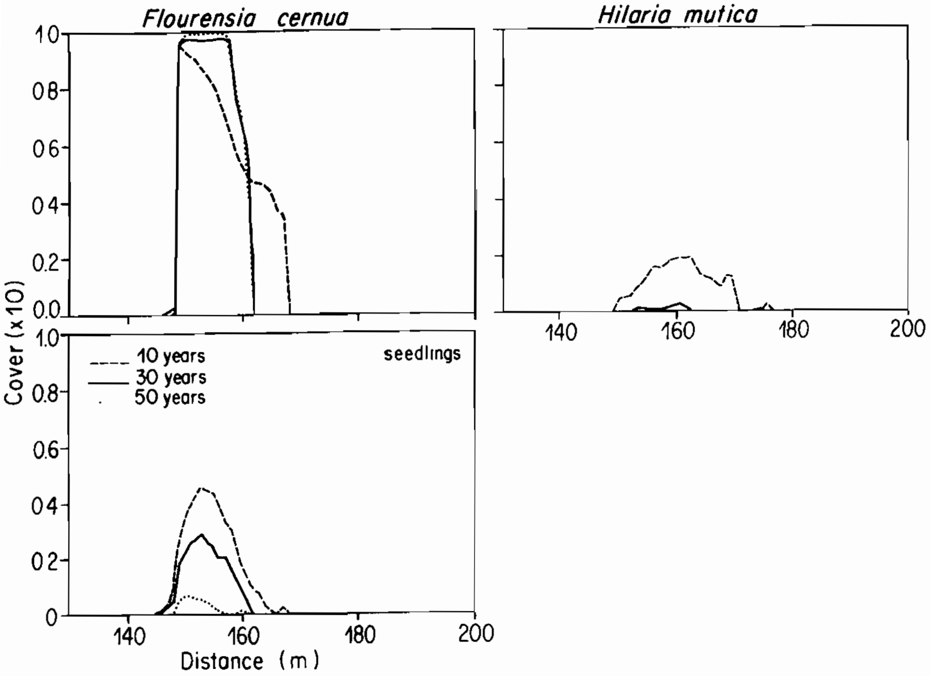

Figure 8.3. Simulation of the changes in both mature and seedling vegetation cover for a stripe composed of two species, the C_4 grass *Hilaria mutica* and the shrub *Flourensia cernua*. The model was run for 50 years, applying a 30% reduction in daily rainfall amounts. The initial conditions used were the average cover of both species observed in the field. No Hm seedlings occurred within the 50-year runs.

minus control by using the procedure proposed by Makridakis and Wheelwright (1978). Annual rainfall decreased by up to 1.13 mm a^{-1} corresponding to a decrease in mean annual rainfall of 85 mm at the end of the 75-year period.

For simulation purposes, we reduced daily rainfall by 30%. This reduction in rainfall caused a dramatic reduction in the vegetation cover for both Fc and Hm (Figure 8.3). The reduction was most pronounced for Hm, which totally disappeared after 50 years. The decrease in Fc cover led to the formation of a narrow band, at the upslope edge of the former band which corresponded to a reduction in vegetation cover of 50%.

Ecosystem-to-Landscape Model

In the previous section, a complex process model was described and used to simulate the dynamics of banded vegetation at the ecosystem scale. Model prediction at this scale addressed issues such as climate change. In this section, we present a much simpler process model that simulates the impacts of disturbances on vegetation bands at the larger landscape scale; climate change impacts are one of the disturbances usefully simulated at this scale (Ludwig and Marsden 1995).

When modeling at the landscape scale, we follow the definition that a landscape unit is composed of two or more ecosystem units linked by their source-sink relationships (Risser 1987). In modeling banded vegetation at the landscape scale, our landscape unit is composed of a repeating series of linked band (sink)–interband (source) ecosystem units extending over an area of a hectare or several hectares. Conceptually, we view banded landscapes as examples of functional heterogeneity, whereby spatial pattern elements are linked by processes mediated by the environment acting at the scale of the band (Kolasa and Pickett 1991). Obviously, heterogeneity per se is so ubiquitous in nature that it needs to be narrowed down to the context of its application. Concepts in ecological heterogeneity have developed over the past four decades to account for innumerable examples of biological variation in time and space, with the degree of heterogeneity varying with the scale of measurement in time and space (Kotliar and Wiens 1990). Kolasa and Pickett (1991) have elaborated a wide range of definitions of patches, boundaries, and examples of heterogeneity; banded vegetation is but one example. The modeling of banded landscapes requires a pragmatic selection from all these heterogeneity concepts, with a focus on the hypotheses to be addressed.

In this section, we examine hypotheses about the potential impacts of land degradation and climate change on banded landscapes located in a semiarid region of Australia. The vegetation of Australia has undergone many changes under the impacts of humans, particularly since its settlement by European farmers and pastoralists (Saunders, Hopkins, and How 1990). It is estimated that some one-half million square kilometers (about 8%) of Australia's semiarid rangelands have undergone "severe" desertification, defined as areas in "poor" range condition with signs of severe soil erosion (Mabbutt 1978; Dregne 1983). The hypothesis is that these degraded semiarid banded landscapes will have lower productivity due to a decline in their ability to conserve resources; our landscape model explores the potential magnitude of such declines.

Global climate modelers have used the El Niño southern oscillation (ENSO) phenomenon to predict rainfall in various regions of eastern Australia to help land managers minimize economic risks and reduce ecological impacts on their lands (Muchow and Bellamy 1991) These risks and potential impacts are greatest in the drought-prone arid and semiarid regions of Australia, which are also most likely to be affected by ENSO-related changes in climate (Nicholls 1991). For semiarid eastern Australia, predictions for the next 30 years are that landscapes in this region could experience higher temperatures, lower winter rainfalls, and higher summer rainfalls, which are likely to occur in fewer but more intense storms. The landscape model examined the potential impacts of such a climate change scenario on the conservation of resources, and hence productivity, for semiarid banded landscapes in eastern Australia.

Landscape Design and Structure of the Landscape Model: Banded Landscapes in Eastern Australia

In semiarid eastern Australia, banded groves of mulga trees (*Acacia aneura* F. Muell. ex Benth.) are commonly interspersed with open, sparsely grassed interbands (Tongway and Ludwig 1990; Ludwig and Tongway 1995). Schematically, in a top-down view, a banded mulga landscape unit has a number of discrete elongated vegetation patches or bands dispersed across gentle slopes of less than 1%, with the bands separated by interband open areas (Figure 8.4). As indicated by arrows, runoff from intense rainfall events will flow down these slopes and out of the landscape unit unless a band captures it. Runoff not captured by the banded landscape unit is termed *runout*.

Landscape banding functions to optimize plant production by concentrating and conserving limited water and nutrient resources (Tongway and Ludwig 1997a). This optimization is based on the theory that arid and semiarid lands function as runoff-runon or source-sink systems (Noy-Meir 1981). This source-sink theory predicts that in arid and semiarid environments with limited resources, productivity will be higher per unit area if resources are concentrated into bands than if uniformly dispersed over the landscape.

Landscape studies around the world have documented that physical processes such as surface winds and surface water flows (runoff) that redistribute resources into bands (Schlesinger et al 1990; Montaña 1992). For example, runoff water recharges soil water in bands, sediment entrained in runoff recharges soil nutrient pools in bands, and wind-blown litter goes to build soil organic carbon in bands (Tongway and Ludwig 1997a). Biological and chemical processes within bands help to maintain them. For example, plants within a band use water and nutrients for growth, and these resources recycle back to the band through death and decomposition (Hodgkinson and Freudenberger 1997). Such dynamic landscape band processes can be modeled (Mauchamp, Rambal, and Lepart 1994), along

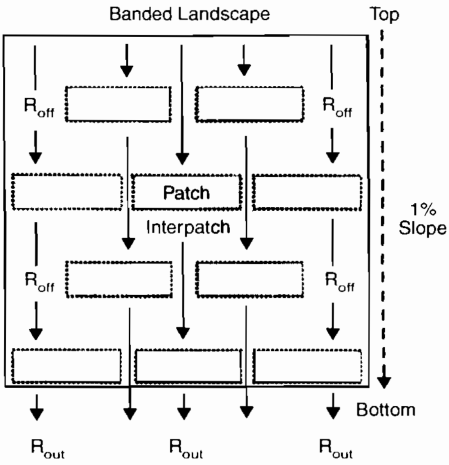

Figure 8.4. Top-down view of a typical semiarid banded landscape in eastern Australia with bands separated by open interband areas. (From Ludwig, Tongway, and Marsden 1994.)

with the vital role of bands acting as "filters" to capture and conserve the scarce water, nutrient, and carbon resources within semiarid banded landscapes (Ludwig, Tongway, and Marsden 1994).

Flow-Filter Landscape Model

A "flow-filter" landscape simulation model was developed to quantify how runoff flows through and possibly out of a banded landscape (Figure 8.5). The flow-filter landscape model has been previously described (Ludwig, Tongway, and Marsden 1994, 1999), so its design and structure are only briefly outlined here. If the amount and intensity of precipitation (P) exceeds the water infiltration rate (I) or water storage capacity (C_s) of the soil within an interband source area, then runoff (R_{off}) occurs. This R_{off} can be "filtered out" by bands of patches within the landscape unit, or if the I and C_s of the patch are exceeded and the band is at the bottom edge of the unit, then runout (R_{out}) occurs from the landscape unit. In functional form, these relationships are

$$R_{\text{out}} = f(P, I, C_s, A_p, A_l)$$

Note that the total R_{out} from a landscape unit following a rainfall event at time t is also a function of the total area of band (Ap) and area of interband (A_l).

Aboveground net plant production (ANPP) for the landscape system was estimated by using a spatially linked forage production simulation submodel called SEESAW (Ludwig, Sinclair, and Noble 1992). SEESAW computes ANPP through

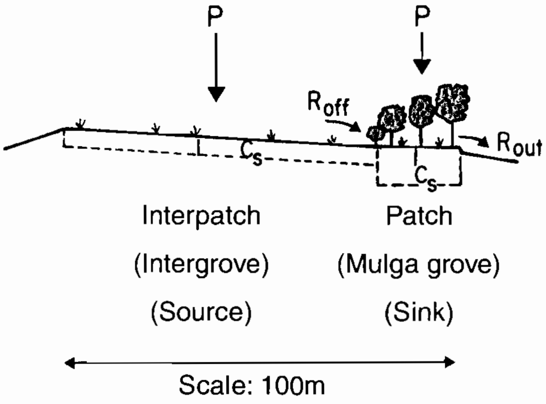

Figure 8.5. Cross-section of a typical semiarid mulga woodland landscape in eastern Australia. The flow of resources is depicted following a precipitation event (P) with runoff (R_{off}) occurring when the amount and intensity of precipitation exceeds the infiltration rate (I) or the water storage capacity (C_s) of the soil. Resources not captured by the band runout (R_{out}) of the landscape (from Ludwig, Tongway, and Marsden 1994). *Note:* soils under banded mulga are deeper, thus having greater C_s, and also have a higher I.

time as a function of plant available moisture (M_a), available nutrients (N_a), and temperature (T):

$$\text{ANPP} = f(M_a, N_a, T)$$

M_a is estimated by another submodel, called WATDYN, which computes soil water balance dynamics on a daily time-step (Walker and Langridge 1996). ANPP was computed for four plant guilds or functional groups: ephemerals (forbs and grasses), C_3 grasses, C_4 grasses, and shrubs. Processes of plant growth, senescence, death, decay, and consumption by grazing animals are incorporated into these computations. Given starting biomass values for leaf, stem, and root components for each plant guild within each landscape band and interband unit, ANPP was computed by using a weekly time-step within each year of a simulation run.

Model Simulation Runs: Scenarios

The simulations used a semiarid landscape scaled system of fixed size, shape, and band structure. For simplicity, we assumed an area of 100×100-m size and of 1% slope, with bands occupying 30% of the area. Semiarid woodland landscapes in eastern Australia typically have bands of mulga tree groves occupying about 30% of the surface area (Tongway and Ludwig 1990). It was assumed that patches were dispersed in bands of a regular pattern over the landscape unit (see Figure 8.4). Banding pattern influences the way runoff is captured within a landscape, which will, in turn, affect ANPP (Ludwig, Tongway, and Marsden 1999).

Three scenarios were simulated: (1) an undegraded or natural semiarid banded landscape; (2) a similar but degraded banded landscape; and (3) the natural banded landscape being affected by climate change. Parameter sets for each of these three scenarios (Table 8.2), included differences in rainfall inputs, soil infiltration rates (I), and soil water storage capacities (C_s) as dependent on soil depth. The parameter values for the natural and degraded landscape systems are based on field measurements in the semiarid mulga woodlands of eastern Australia (Greene 1992). The rainfall and temperature data used as inputs for the simulation runs were based on a 31.5-year record from mid-year 1962 through 1994 collected from a class A weather station at Cobar, New South Wales, located in the heart of the semiarid woodlands of eastern Australia. The climate change scenario modified this data to include a 2°C rise in average annual temperature, a 10% drop in mean winter rainfall, and a 10% rise in mean summer rainfall. Summer rains were modified to occur in fewer but more intense events.

Landscape-Level Predictions

The natural banded mulga landscape had an average ANPP of about 33 g dry matter (DM) m^{-2} over the 31.5-year simulation run (Figure 8.6a). By contrast, ANPP for the degraded landscape only averaged about 16 g DM m^{-2}, about half that of the natural landscape. This was most likely due to the degraded landscape losing a far greater amount of rainfall as R_{out} (Figure 8.6b). However, relative to these

Table 8.2. Data and Parameter Values for Three Scenarios Used to Simulate the Impacts of Land Degradation and Climate Change on Semiarid Banded Landscapes in Eastern Australia[a,b]

	Scenario		
Data and parameters	Natural landscape	Degraded landscape	Natural landscape and climate change
Precipitation data from Cobar (NSW)	Actual*	Actual	+10%S and −10% W[c]
Infiltration rate I (mm h^{-1})			
Band	60	30	60
Interband	10	5	10
Soil depth Cs (cm)			
Band	100	75	100
Interband	45	30	45

[a] Typical infiltration rate and soil depth parameters for within patches and interpatches are from Greene (1992)

[b] Actual rainfalls for events from mid-year 1962 through to the end of 1994.

[c] S, summer (Dec to Feb). W, winter (Jun to Aug)

natural and degraded landscape scenarios, the impact of a changed climate was to increase ANPP, to 42.5 g DM m^{-2}, probably due to these landscapes capturing more runoff water.

One hypothesis that we examined is that climate change will shift plant guild composition (Nicholls 1991). Our simulations support this hypothesis by predicting that C$_4$ grasses significantly increased their ANPP under the climate change scenario compared with the natural system (Figure 8.7), whereas other plant guilds

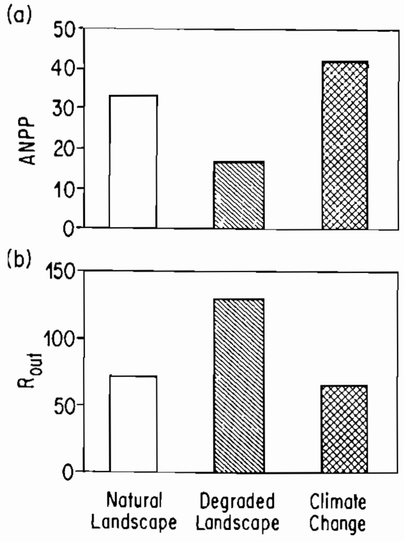

Figure 8.6. (a) Mean annual aboveground net plant production (ANPP) (in g DM m^{-2}). (b) Mean annual loss of runoff (R_{off}) (in mm of H_2O) simulated over a 31.5-year period (mid-1962 to 1994) for three landscape scenarios: natural, degraded, and climate change.

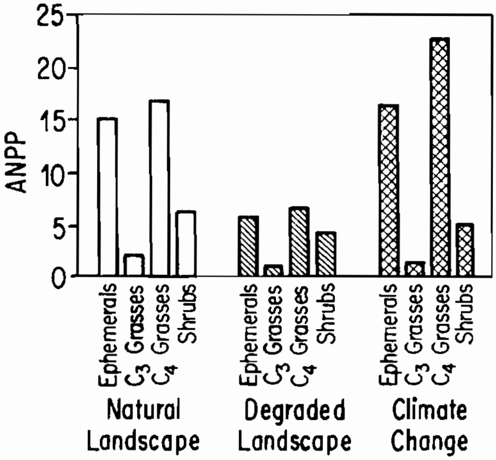

Figure 8.7. Annual aboveground net primary production (ANPP) (in g DM m $^{-2}$) for four functional plant groups averaged over a 31.5-year period (mid-1962 to 1994) for three landscape scenarios: natural, degraded, and climate change.

showed little change. However, these C_4 grasses significantly declined when subjected to degradation (i.e., lowered resource capture at the band scale), as did other plant guilds, except for shrubs, which declined only slightly.

The increase in C_4 grasses predicted by this simulation study for the climate change scenario might be expected from a knowledge of the adaptive responses of plants with the C_4 photosynthetic pathway (Hattersley 1992). Compared with plants with the C_3 pathway, the C_4 pathway produces a higher rate of photosynthesis for a given CO_2 level when climatic conditions are warm and dry and light intensities are high. Thus, a scenario of warmer temperatures with greater summer rainfall favors the C_4 grasses more than the C_3 grasses and forbs.

Landscape Management Implications

These modeling results suggest that the potential impacts of land degradation are far greater than any impacts expected from climate change, at least for banded landscapes in semiarid eastern Australia. When resources such as water and nutrients, which are limiting in these landscapes, are lost due to degradation, significant declines in plant production can be expected, particularly for forbs and grasses, perhaps less so for shrubs and trees. Land degradation (e.g., caused by high grazing pressure) is known to cause a loss of bands in these banded woodlands (Tongway and Ludwig 1997b), thus causing a decline in the capacity of these systems to capture resources. Banded shrublands in arid Australia appear to be robust to grazing pressure based on another modeling study (Dunkerley 1997), although less so under drought conditions.

These simulations of disturbances on banded landscapes also suggest that to rehabilitate degraded areas, landscape patches must be restored through appropriate land management practices, including the application of rehabilitation treatments. An effective treatment now known to speed the restoration of landscape patches is the construction of surface obstructions to water flows (along contours) with tree and shrub branches (Ludwig and Tongway 1996; Tongway and Ludwig 1996). This restores both the means and the processes, which capture the limited vital resources of water and nutrients and thus recreates fertile bands.

Beyond the Hillslope: Discussion

Representing the functioning of a complex system, a vegetation band and its associated hillslope and landscape, requires that a large number of processes and parameters are represented in a modeling exercise. The accuracy of available data and the means for checking the simulation results demand a compromise between simplification and realism that we have attempted to meet in both exercises.

By integrating the systems modeled into a larger watershed, the simulated results could have several implications at a landscape scale:

1. As the system modeled is not closed (see Figure 8.4), each band is likely to receive an additional input of water from upslope that may modify the predictions of the model and particularly limit the downslope retreat.
2. Vegetation bands are usually located on the slopes of endorheic basins (baja) in which a high proportion of the runoff is lost by evaporation from the surface of open water bodies or used by grasslands growing in these low areas. The infiltration of water in the bands reduces runoff, and the resulting dense vegetation cover suggests improved water use for biomass production at the hillslope scale only. Extrapolation at the landscape scale needs to be carefully verified.
3. Processes not simulated, such as disturbances or dispersal of seeds between successive bands, could lead to particular patterns of species distribution (e.g., upslope gaps in the tree cover, which would allow the growth of grass). Such patterns could strongly influence the outcome of the simulations. They could also lead to differences between two bands or two neighboring transects within the same band.

In the two modeling exercises described in this chapter, we focus on processes that controlled both plant productivity and the dynamic budgets of energy and matter at three spatial scales. For a whole-landscape analysis and the approaches related to the notion of "provision of ecosystem services to humans" (Chapin et al. 1997), we cannot neglect the relatively high productivity of the lower-lying grassland areas, which depend in part on water flowing from upper less productive areas and surrounding hillslopes. We simulated the flow of water and carbon in such a grassland with a model that is an upgrade of early versions developed by Rambal and Cornet (1982) and Mougin and associates (1995). The vegetation in low areas of the Mapimi Reserve is largely dominated by Hm, a keystone species in the functioning of the vegetation bands (see above). We compared two contrasting scenarios. The first scenario simulated the effect on function of lateral water flows coming from banded hillslopes ($R_{out} \neq 0$, see Figure 8.4), and in the second we assumed $R_{out} = 0$. In the second scenario, the only water available for plant growth was incident rainfall. With R_{out}, the annual amount of infiltrated water reached on average 433 ± 116 mm, whereas without R_{out}, it was only 284 ± 65 mm. The corresponding plant productivity was analyzed through the comparison of aboveground biomass. With R_{out}, live biomass production ranged from 100 to 320 g DM m^{-2} depending on the year. Stopping R_{out} inflows induced changes in the plant productivity. It decreased progressively from 60 g DM m^{-2} in wet years to quasi-stable low values of 15 g DM m^{-2} in normal and dry years. Changes in the water budget had a drastic effect on plant productivity and highlighted the nonlinear nature of the relationships between water resource and productivity in arid and semiarid environments at all spatial and temporal scales (Yair and Danin 1980; Schlesinger and Jones 1984; Schlesinger, Fonteyn, and Reiners 1989).

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9. Landscape Models for Banded Vegetation Genesis

Jean M. Thiéry, David L. Dunkerley, and Blair Orr

Introduction

Great interest has been paid to the genesis of banded vegetation, with various hypotheses on their evolution: the pattern could have been derived from a previous denser structure through climatic or anthropic degradation (White 1971) or from a bare area through gradual colonization by vegetation that traps sand and organic materials (Boudet 1972). White (1970) speculates termites may play a role in initiation of the pattern.

Various theories have been developed to answer critical questions:

1. How does *brousse tigrée* form, and specifically, can it form from a random pattern of vegetation submitted to decreasing rainfall?
2. Do vegetation bands move uphill as suggested by Ambouta (1984) or evidenced in other banded vegetation (Mauchamp et al. 1993) or remain stationary as suggested by Wickens and Collier (1971) and Mabbutt and Fanning (1987)?
3. What are the processes involved in the bare area colonization, if it does exist?
4. Is water use optimized?
5. What are the management implications? Especially, what happens if one plants vegetation in the bare bands? If the bare bands are necessary for the survival of the plants in the vegetation bands, will planting disrupt a key ecosystem process and lead to a net loss of biomass (Orr 1995)?

Modeling of ecological systems can be developed at different scales. This chapter focuses on long-distance modeling (i.e., at the landscape scale [on distances above 100 m with a resolution above 1 m]). Other models with more detailed mechanisms are described in this book, especially by Mauchamp and colleagues (chapter 8, this volume).

The first part of this presentation focuses on landscape models with actual or potential application to banded vegetation. Only the most pertinent publications have been selected to exemplify the main trends in this research field. Many other important publications could be found in general reviews by Baker (1989), Turner and Gardner (1991), Vanclay (1995), or Shugart (1998).

The second part discusses recent developments of landscape models with different formalisms currently applied to banded vegetation in semiarid regions.

Review of Landscape Models for Banded Vegetation

In his general review of landscape models, Baker (1989) has defined three types of models: whole landscape models, distributional landscape models, and spatial landscape models.

In "whole landscape models," the landscape state is summarized by only one number, which could be the percentage of vegetated soil in banded vegetation.

In "distributional landscape models," the main information is represented by a histogram, which for example, could give the mean water infiltration in bare and vegetated bands.

In "spatial landscape models," the detailed information is usually predicted on a regular grid, whereas the measured data are recorded either on a regular grid (e.g., by remote sensing) or on specific points (e.g., by data recorders). A typical output of such a model could be a vegetation density map.

In the same review, models are also differentiated by their respective treatments of space and time. Both of these dimensions may be discrete or continuous, with proper mathematical formalisms such as

difference equations (distribution models with discrete time)
differential equations (distribution models with continuous time)
cellular automata (regular spatial grids with discrete time)
partial derivatives (continuous space and continuous time)

The classification of Baker (1989) can be adapted to banded vegetation. In that case, whole landscape models can be divided into qualitative conceptual models and into descriptive landscape heterogeneity models. Spatial landscape models may be represented in one dimension as transect models or in two dimension as spatially explicit models.

Conceptual Models

Banded vegetation studies present an interesting case of a scientific discipline that has been developed for many years with little or no mathematical formalism. In fact, the first models were purely conceptual and could be described in vernacular language, eventually with the help of a photograph or a simple sketch.

One of the first models of the initiation of vegetation bands on gentle slopes in semiarid climates was presented by Greig-Smith (1979). This simple conceptual model already led to many qualitative predictions such as the asymmetry in tree densities between the well-watered upper edges and the dryer downslope edges, the lateral extension of initial patches into large bands and the upslope migration of these bands.

Ambouta (1984) presented a more detailed conceptual model of *brousses tigrées* in Niger, with five specific zones (later called *degraded, runoff, sedimentation, pioneer front, central,* e.g., in Thiéry, d'Herbès, and Valentin [1995]). This model also emphasized the important role of termites and pioneer plants.

The success of these simple conceptual models is partially due to the existence of positive feedbacks. Once started, a positive feedback process has an autocatalytic effect, often with an exponential growth phase until the onset of limiting processes. The global effect is represented by a sigmoidal curve and allows the transition from one state to another one. Wilson and Agnew (1992) have introduced the term *positive feedback switch* (or simply *switch*) for processes in which a community modifies its environment, making it more suitable for that community. These switches may explain many stable mosaic situations, in which two communities modify their local environment in their favor. Wilson and Agnew (1992) have described numerous vegetation switches mediated by water, soil, light, temperature, wind, fire, allelopathy, microbes, termites, herbivores, and so on. Some of these factors (e.g., water, soil, wind, and termites) play an important role in the genesis of banded vegetation patterns.

Schlesinger and co-workers (1990) emphasized the importance of biological feedbacks in global desertification. Their conceptual model for desertification explains how long-term grazing of semiarid grasslands leads to an increase in the spatial and temporal heterogeneity of water, nitrogen, and other soil resources. The replacement of grass by shrubs favors greater erosion in the barren area between shrubs. These processes have been well studied in the Sahel and in the Chihuahuan Desert. But in the same regions, an increase in heterogeneity may also lead to a greater resistance to climate stress, as shown by *brousses tigrées,* which, on gentle slopes, are able to limit erosion (Clos-Arceduc 1956; Cornet, Delhoume, and Montaña 1988).

Descriptive Landscape Heterogeneity Models

Natural landscapes may appear heterogeneous, at different scales depending often on the species studied (microbes, insects, or higher vertebrates) and their habitats. Milne (1992) has introduced different criteria to quantify this multiscale heterogeneity. His approach, based on the fractal theory (Mandelbrot 1982), was tested on natural landscapes as well as on artificial ones with random, checkerboard, or sinusoidal patterns. "Sinusoidal patterns" could be an approximation for banded vegetation patterns. True vegetation bands present a characteristic periodicity, which is not compatible with a fractal model at the global level (i.e., >100 m). However, "fractal models" could apply at lower scales on the vegetation band boundaries (capes and bays) or within vegetated bands (e.g., trees, roots). They could also apply in transition regions where bands are disordered.

In arid regions where plants cover only a fraction of soil, the heterogeneity scale may be of the order of 1 m in the case of scattered plants or trees (e.g., in natural bush or in cultivated areas such as cotton fields). The heterogeneity scale may be much larger (up to 100 m in extent) in the case of patchy woodlands or of *brousses tigrées.*

Most landscapes are heterogeneous at greater scales (>1 km). This variability has large effects on heat and moisture fluxes and should be taken into account in climate models (Pielke et al. 1993). Similar effects are probably important in arid regions (e.g., *brousses tigrées* plateaus surrounded by cultivated or fallow depressions).

"Random landscape" models are often used as "neutral" models, depending on a small number of parameters and allowing the prediction of general trends. Turner and associates (1989) have used such a model to predict the spread of disturbance across heterogeneous landscapes, within the framework of percolation theory. Disturbances are characterized by their frequencies and their intensities while random landscapes are defined by their probability of occurrence of disturbance-prone habitat. Trends are different below or above a "percolation threshold" for this probability. Below this threshold, disturbance frequency is more important than disturbance intensity, whereas the reverse is true above the threshold.

Distributional Models

One of the simplest ways to take into account the landscape heterogeneity at a given scale is to classify each separate parcel into a small number of categories. For example, Frelich and Lorimer (1991) introduced eight structural types for hardwood stands in a primary forest in Upper Michigan. Natural growth and storm disturbances introduce transitions between these structural types. The complete landscape is described by the percentage of stands within each type and can be represented by a simple histogram at any given time. Changes in storm frequencies and intensities modify this stand distribution, which may be different from a steady-state repartition under constant climate. Such a model, with a finite number of states connected by transition probabilities, is called a Markov chain model (Baker 1989).

For Sahelian landscapes, Hanan, Prince, and Hiernaux (1991) have introduced a multicomponent or "checkerboard" model. Each landscape unit is described by its fractions of typical components such as *brousse tigrée,* patchy woodland, or cultivated or fallow depressions. This distributional model has been applied to remote sensing data usually summarized by the normalized difference vegetation index (NDVI), defined and optimized for homogeneous vegetation. In heterogeneous landscapes, the measured NDVI is a function of the brightness, of the NDVI and of the fractional cover of each component. Hanan, Prince, and Hiernaux (1991) have shown how the true vegetation NDVI can be computed from the global landscape NDVI.

For plant species, Noble and Slatyer (1980) have introduced the "vital attribute classification" based on critical times such as the time to reach reproductive maturity, the longevity of the species population, and the longevity of the propagule pool. This classification permits one to predict changes in community composition with changes in disturbance regimes (e.g., fires or floods).

Transect Models

Ecological functional models synthesize the most important elementary processes explaining the ecosystem evolution. They can be space-independent distributional models describing the evolution of average demographic or ecophysiological variables (Desanker and Prentice 1994; Vanclay 1995). They can also be spatialized at the landscape scale, possibly in three dimensions (latitude, longitude, and altitude with soil depth and/or atmosphere height). For terrains with a uniform slope, modeling may often be restricted to a transect (which drastically reduces computation time).

Mauchamp, Rambal, and Lepart (1994) have published a transect functional model simulating the dynamics of a tiger bush in Mexico. Ludwig, Tongway, and Marsden (1994) have developed a two-component model with runoff and runon zones acting, respectively, as water sources and sinks. These zones are distributed on a gradsect (i.e., a gradient-oriented transect) (Gillison and Brewer 1985). These two models are developed in Mauchamp and colleagues (chapter 8, this volume), with other synthetic models of functioning.

Spatially Explicit Models

Static landscape models can be easily described with appropriate geographic information systems (GIS) and proper programming languages. Dynamic landscape models require a complete description of population dynamics, including reproduction, development, and survival. Plant seed dispersion and animal migrations should also be included. Pulliam, Dunning, and Liu (1992) published a detailed presentation of such a model. Their model simulates the effect of timber harvest management on the size and extinction probability of avian populations. Their simulations suggest that variation in demographic variables affects population size more than variation in dispersal ability.

Baker, Egbert, and Frazier (1991) developed a general modeling tool for the simulation of landscapes subject to large disturbances. This tool (DISPATCH) can simulate

1. effects of repeated disturbances in a landscape over hundreds of years
2. effects of spatial variation in the environment on the probability of disturbance initiation and spread
3. the interaction between landscape structure and disturbance initiation and spread

4. effects of climatic changes
5. quantitative changes in landscape structure

It combines a general SIMSCRIPT II.5 simulation language with a GIS, a statistical package and a graphical software. Such an approach requires large computing times (e.g., 8 h for a single run on a classical UNIX work station at 12.5 million instructions per second).

Coughenour (1992) developed a spatially organized dynamic ecosystem model, called SAVANNA, for the study of landscape heterogeneity and of the migration patterns of the nomadic herdsmen. Monthly vegetation indices and other GIS data were used for inputs and verification. The model demonstrated the importance of pastoral mobility as a strategy for dealing with temporal changes in forage availability. It also showed how water redistribution in the landscape affects vegetation and ecosystem dynamics, resulting in relatively productive patches within an arid system.

Spatially explicit models may be used to simulate landscape changes after periodic or random disturbances such as fire or storms. Many of these models use the framework of cellular automata. In this formalism, the landscape is divided into cells and the model introduces an interaction matrix between neighboring cells. The interaction matrix may be isotropic, as in the original "game of life" of J.H. Conway (1976), or anisotropic when the disturbance is oriented by wind or water flow.

Hochberg, Menaut, and Gignoux (1994) used a cellular automaton to simulate the role of fire on the savanna-forest equilibrium in West Africa. In the absence of any directional effect, their interaction matrix is isotropic and takes into account the protection of a given seedling by neighboring trees (all trees are assumed to be of the same species). The model also introduces classical plant population parameters for dispersion, germination, and survival. Under these assumptions, fire reinforces the clumped distribution of trees and slows down the rate of tree spread in humid savannas. Sensitivity analyses emphasize the effect of seed dispersal, which increases the spread of trees across the landscape.

Cellular automata can be used to simulate long-term landscape organization due to water flow or dominant winds. These automata are anisotropic and are oriented in the direction of local fluxes. They have been applied to differently organized landscapes from boreal mires (Swanson and Grigal 1988) to semiarid tropical *brousses tigrées* (Thiéry, d'Herbès, and Valentin 1995; Wiegand, Milton, and Wissel 1995; Orr 1996; Dunkerley 1997a,b). Recent developments on automata of this type are discussed in the following sections.

Cellular automata may also be used to simulate short-term landscape changes induced by fire, storms, or epidemics. Feunekes and Methven (1988) introduced a specific time-dependent anisotropic cellular automaton to simulate fire propagation in a heterogeneous landscape. The automaton anisotropy depends on wind direction and is not constrained by the landscape representation on a Cartesian grid. The automaton intensity varies with agrometeorological data such as wind speed, temperature, relative humidity, and accumulated rain. Fire propagation is simulated for many days with a time-step equal to 1 hour, due to large daily variations in fire spread (possibly 10 times greater in the afternoon than at night). The original computations were run on PCs of the first generation, which emphasizes the relative efficiency of cellular automata with respect to computer time.

Models based on individuals are now used more frequently in both ecology and economics. They are well adapted for modeling population behavior in terms of individual strategies for reproduction, dispersion, and resource management. They have been used to simulate many types of collective or social behaviors for ants, fish, or men (Lepage and Mullon 1994). Such an ensemble of interacting individuals is called a multiagent system. With high-speed work stations, researchers can test many hypotheses on individual strategies leading to global behaviors similar to or different from reality. This domain of research is called artificial life.

As an example, Liu (1993) has developed an ECOLogical-ECONomic model (ECOLECON) to simulate animal population dynamics and economic revenues in response to different forest landscape structures and timber management scenarios. ECOLECON is a spatially explicit, individual-based, and object-oriented program. It can be linked to GIS to run simulations on real landscapes. The synthesis of ecological and economic concerns represents an expanding new field of research with its own journals such as *Ecological Economics* or *Forest Ecology and Management*. Interesting information on this subject and on decision support systems can be found on Internet with keywords such as *ECOLECON* or *ecology and economics*.

These recent developments of ecological models often use object oriented languages (e.g., smalltalk, C++, and now, Java), allowing a good description of hierarchies in ecological data (e.g., a given tree may belong to a grove within a forest and to a species within a genus).

Spatial self-organization (as found in banded vegetation) is a general property of many biological, chemical, or physical systems. It results from detailed interactions between cooperative and competitive effects. Lejeune and Lefever (1996) have developed a mathematical model to explain the formation of *brousses tigrées* (integro-differential formalism reducible to partial derivatives, i.e., with continuous space and continuous time). This model takes into account the cooperative vegetation reproduction, the competition for resources, and the vegetation death or destruction. Its conclusions are general. Vegetation patterns may occur even under isotropic environmental conditions. Under anisotropic conditions, vegetation bands may be oriented either perpendicular or parallel to the anisotropy direction. Arc-shaped patterns, like dunes, may occur in some cases.

Recent Developments in Banded Vegetation Models

Five spatially explicit landscape models have recently been proposed for banded vegetation patterns. Three of them use the cellular automata formalism. The TIGREE model (Thiéry, d'Herbès, and Valentin 1995) is global and uses only two main parameters for competitive and synergistic plant interactions. The second model, RUNONOFF (Dunkerley 1997a,b), introduces, at the same scale, a more detailed description of water distribution. The third model, TGRBR (Orr 1996), takes into account the competition between trees and grass for water resources. Two other models using a continuous formalism have been developed by Lejeune and Lefever (1996) and by Klausmeier (1999). Some recent developments of these models are presented in the following sections.

TIGREE and TIGRFLUX Models

The TIGREE model (Thiéry, d'Herbès, and Valentin, 1995; d'Herbès, Valentin and Thiéry 1997) is derived from the "game of life" (Conway 1976) and depends on only two hypotheses that reflect competition and synergy: the establishment, growth, and survival of a given plant are affected negatively by plants situated upslope and positively by lateral and downslope plants. In the cellular automata formalism, these interactions are represented by an "interaction matrix," depending on only two coefficients: the a coefficient reflecting "upslope resource competition" and the b coefficient reflecting "lateral synergy." This model can be easily programmed as Java applets embedded in HTML pages (Thiéry et al. 1998).

The original TIGREE model was built to simulate the evolution of vegetation on a sloping semiarid plateau. This model can be easily modified to simulate a horizontal plateau with the following interaction matrix:

$$\begin{array}{ccccc} -a & -a & -a & -a & -a \\ -a & b & b & b & -a \\ -a & b & * & b & -a \\ -a & b & b & b & -a \\ -a & -a & -a & -a & -a \end{array}$$

where the a coefficient reflects the "competition for resource" (especially water) and the b coefficient reflects "synergy" between plants. This matrix represents nearly isotropic interactions because interactions are the same in two perpendicular directions, but they are not identical in the main directions and along their diagonals. There is a rotation axis of order 4 (C_4) in this symmetric model TIGRSYM. We have run this model with a and b values close to the original ones (Thiéry, d'Herbès, and Valentin 1995). All other equations and secondary parameters were the same as in the original publication ($B = -1$; $H = 1$, and $c = 0.4$). For $b = 4$, we obtain successively a full vegetated plateau ($a \leq 1.2$), a vegetated plateau with some bare spots ($a = 1.3$), a "maze" with bands oriented preferentially in x or y but also in other directions ($a = 2$), and nearly random vegetation spots ($a = 4$). The changes in a could represent the transition from a Sudanese climate to a Sahelian climate.

In the TIGREE model, like in most cellular automata for banded vegetation, landscape is represented by a rectangular grid well adapted to sloping plateaus with two principal directions. For comparison purpose, horizontal plateaus may also be represented by rectangular grids, where isotropic interactions can be approximated with C_4 matrices, with or without optimized coefficients. This approximation introduces some systematic bias in the orientation of computed landscapes but probably not on their topology. Better isotropic representations of horizontal plateaus would be on hexagonal grids, but these are unfortunately less well adapted to sloping plateaus. Schönfisch (1997) has compared the influence of different random grids on the anisotropy in cellular automata. Some of them could be used to properly represent horizontal and sloping plateaus.

On all landscapes, plants compete for light, water, and limiting nutrients. But in semiarid regions, plant competition is mainly for water. Galle, Ehrmann, and Peugeot (1999) have measured water balance in a western Niger *brousse tigrée.* Their results have been integrated into a new landscape model called TIGRFLUX (Thiéry et al. 1997). TIGREE and TIGRFLUX are similar except for the description of water competition. In both models, the landscape is divided into cells (about 5 m * 5 m) with four possible states representing the biological activity (state 0 for bare cells, state 3 for fully active vegetation, states 1 and 2 for intermediate activities). Interactions between cells are represented by an interaction matrix with positive, null, or negative values in TIGREE and with positive or null values in TIGRFLUX, where the interaction matrix introduces no competition. In TIGRFLUX, competition effects are described by a detailed computation of water fluxes. As an extrapolation of experimental results, the runoff from each cell is assumed to be a linear function of the incoming water flux (rain and runon) above a minimum threshold. The linear parameters depend strongly on the soil surface (i.e., on vegetation). The evapotranspiration of each cell is a function of the cell state and of the neighboring cell states (through the interaction matrix): evapotranspiration is lower in cells surrounded by vegetated cells than in cells surrounded by bare cells. In the absence of deep drainage, the future evolution of each cell depends on the balance between evapotranspiration and infiltrated water. TIGRFLUX introduces more parameters than TIGREE, but most of these new parameters can be checked experimentally. Preliminary results of TIGRFLUX are promising, but systematic comparisons with experimental data are still necessary for a complete validation of this model (Thiéry 1997; Thiéry et al. 1997).

TIGREE and TIGRFLUX do not take into account detailed mechanisms for competition and synergy (except for water competition in TIGRFLUX). A complete analysis of relevant phenomena has recently been published by Ehrmann (1999). This analysis could lead to a complete model for Nigerien *brousses tigrées,* similar to the TLALOC model developed by Mauchamp, Rambal, and Lepart (1994) for Mexican vegetation mosaics.

The TIGREE model is a synthetic model well adapted to long-term studies. As shown in the original publication (Thiéry, d'Herbès, and Valentin 1995), its two main parameters can be easily estimated with statistical analyses of aerial photographs. This model could be used for forest management (d'Herbès, Valentin, and Thiéry 1997; Thiéry, d'Herbès, and Valentin 1997). For example, two types of management have been compared: reforestation of the bare zones versus wood harvesting and optimized regeneration. Reforestation of the bare zones (without catchment construction) is not sustainable and newly planted trees die rapidly. Catchment in the bare zones will introduce large runoff perturbations that cannot be directly tested by TIGREE and that will probably destroy the downhill pioneer zone. This question is discussed more thoroughly in the section on the TGRBR model. Wood harvesting in the degraded zone favors the development of downhill pioneer zones; regeneration can be accelerated by planting seedlings in the sedimentation zone. Similar management schemes could be tested with TIGRFLUX, which could take into account the impact of catchments. Long-term management experiments, with proper measurements, are necessary for the accurate validation of these simplified management models.

These simplified models could be integrated into general models taking into account long-term economic, technical, population, and societal aspects of sustainable development (Thiéry 1998).

RUNONOFF Model

In this section, simple cellular models of the kind described by Dunkerley (1997a,b, 1999) are explored further. The earlier model used a single unvarying value of the rainfall in every iteration (iterations being interpreted as standing for 1 year). This was done so that any influence of rainfall decline in producing the fragmentation of plant cover, and so possibly influencing mosaic development, was excluded. However, in arid and semiarid landscapes, there is often marked interannual variability of rainfall. Therefore, it is necessary to see whether simple cellular models can generate banded patterns under widely varying rainfall.

It is worth noting that although the tessellation of cells receives rainfall input, the state of each cell nevertheless depends solely on the state of the cells in its neighborhood to which it is linked in the model rules. Therefore, the models explored here do not belong to the group of dynamic automata that has been explored in studies such as that of Wiegand, Milton, and Wissel (1995). In these latter models, cells may possess a degree of autonomy so that their properties may depend on the passage of time as well as on the state of neighborhood cells.

These simple models are also explored further in the context of the nature of water partitioning behavior necessary among adjacent vegetated cells. In the earlier models, the water partitioning rules adopted were as set out in Figure 9.1. This involved water sharing among six cells in the neighborhood of any vegetated cell. Vegetated cells, being sites of efficient water infiltration, were modeled as sources of soil water that could move by seepage laterally as well as vertically. Some of this water would be available beneath an adjacent unvegetated cell, so improving the character of that cell as a potential site for further plant growth.

Here, the nature of this water partitioning is investigated further by varying the extent of water sharing (e.g., among three or six neighboring cells) and by varying the quantity transferred. In the earlier model (see Figure 9.1), a vegetated cell partitioned 45% of its soil water to adjacent cells, irrespective of the size of the

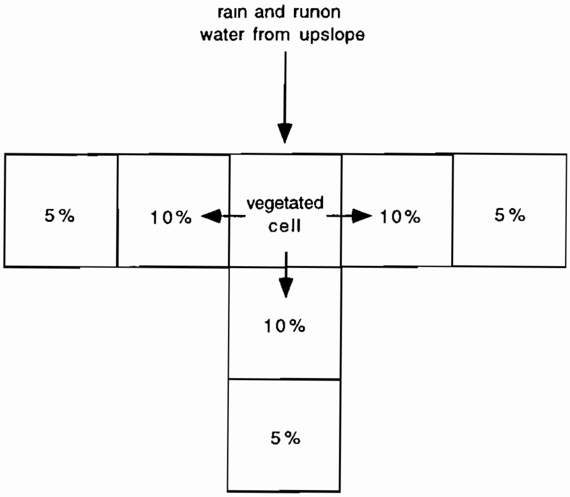


Figure 9.1. Pattern of cells in the neighborhood of a vegetated cell that acts as a source of water. In some trials with the cellular model, the extent of the neighborhood is reduced to three cells rather than six by eliminating the three outermost cells. The figure illustrates the fraction of water apportioned to each cell in the neighborhood.

rainfall event, 15% being partitioned to the two neighboring cells on each of the left and right sides, and 15% to the two neighboring cells downslope. Here, the proportion shared is varied over a wide range to examine the model outcome.

Finally, in the earlier models vegetated cells were modeled as absorbing all water flowing or falling onto them. Here, that stricture is relaxed, and the model response to varying water trap efficiency is observed.

Particular attention will be paid to the effects of the above variations on the geometry of the model-generated banding patterns, in particular to band width and spacing.

Methods of the RUNONOFF Model

The 50 × 50-cell model of Dunkerley (1997a,b) is used for the present trials. As in earlier work with this model, simulations were commenced from a random distribution of vegetated cells. The extent of vegetation cover across the model tessellation was found to have little effect on model behavior, and simulations were therefore begun with a consistent 40% of cells vegetated.

Modifications to the model were as follows:

1. The degree and extent of lateral and downslope water partitioning were made variable. It was reported by Dunkerley and Brown (1999) that the degree and extent of water partitioning might be variable in response to site-to-site variation in the nature and abundance of surface plant litter, for example. Subsoil

permeability would clearly also vary and influence these processes. Further, the condition of the plant communities themselves might be influential. Dunkerley and Brown (1999) envisaged in particular that sequences of wet periods might induce greater leaf production in grasses, changing the response of the landscape in subsequent rain events shortly thereafter. If this kind of response applies, then site water partitioning would indeed be variable temporally as well as spatially.

2. The water infiltration occurring into vegetated cells was made variable. In the case of the vegetation communities described by Dunkerley and Brown (1995), it seemed possible that water might be delivered to vegetation bands in excess of their infiltration capacity, at least in rare events of intense rainfall. Under such conditions, some water might pass downslope beyond the border of a single runoff-runon unit. This would carry the further implication that at least limited sediment transport across the landscape might occur. Ordinarily, banded landscapes of the kind studied in western New South Wales, Australia, appear to be strongly if not completely compartmentalized. In other words, in all but the most extreme rainfalls, water shed from the runoff sources is highly unlikely to pass through the vegetated band immediately downslope, and this leaves the landscape effectively subdivided into binary runoff-runon couplets, with no integrated runoff passing downslope. The microtopography of these landscapes (Dunkerley and Brown 1995) is effective in creating and sustaining these isolated compartments that trap both water and sediments.
3. The rainfall delivered to the tessellation of cells at each iteration was made variable. Because the simple model used here works only with single rainfall values for each iteration, these were generated as required within the model. To reflect the great interannual variability characteristic of many semiarid regions, the values were selected at random from a population of annual rainfall values roughly following a log-normal distribution. The original model used a fixed rainfall of 100 mm per iteration: here, the range spans 50 mm per iteration to 350 mm per iteration. These values represent a distribution similar to that reported for western New South Wales by Bell (1972). He reported that coefficients of annual variability (standard deviation as a percentage of the mean) in this area were 40 to 50%. The rainfall used in the cellular model was scaled downward, preserving the degree of variability, to be able to generate multiple cycles of banding within the 50 × 50-cell tessellation. The actual mean annual field rainfall in the area of western New South Wales where banded vegetation occurs is in the 200 to 250-mm a^{-1} range, although the model uses a value whose mean is 100 mm a^{-1}.

As before, summary data were collected for each model run and for the condition of the plant cover for each iteration within a run. These data were used to examine the effects of the model modifications on the *equilibrium* plant cover achieved across the model once banding, if it evolved, had come to a relatively stable condition. (The extent of model instability in the face of varying rainfall is discussed below.)

Results of the "RUNONOFF" Model

Varying the Amount and Extent of Lateral and Downslope Water Partitioning

The results of trials with varying amount and extent of water partitioning among neighboring cells are shown in Table 9.1.

It can be seen from these data that the fraction of vegetation cover developed in the model increases with the extent of lateral and downslope water sharing among neighboring cells. If the water from a source cell is only partitioned among the three immediately adjacent cells (one to each side and one downslope), the vegetation cover developed is fractionally greater than if the partitioning is among six cells. The smaller amount of water lost to cells one cell removed from the source cell may in part be lost into unvegetated cells, from which any stored water is lost at the end of each iteration. These differences are all significant at the 1% level (using a t-test for difference of means) with the exception of the 5% water-partitioning level, where no significant difference between six- and three-cell neighborhoods is evident. The reason for the lack of significance in this case is made clear below.

It is necessary to consider the spatial arrangement of the vegetation cover in the above experiments. Sharing of 15% and 10% of stored water from a source cell in all cases permitted the development of clear, linear, cross-slope banding patterns. However, as the amount of water shared was diminished to 7.5%, the lateral extent of the resulting bands diminished. Rather than being 50 cells long (i.e., spanning the whole tessellation), the bands remained fragmented, individual bands being perhaps 10 to 15 adjacent cells in length (Figure 9.2). With only 5% of water shared, band development was greatly restricted. Plant cover under these conditions consisted more of small patches aligned across the slope, of perhaps no more than five adjacent cells in length. Under these circumstances, the benefit of water partitioning among neighboring cells is greatly diminished, and no statistically significant difference between the tessellation vegetation cover for the three- and six-cell neighborhoods was found, as noted above (only three cases are shown for clarity).

Table 9.1. Effect of Varying Spatial Extent and Amount of Water Partitioning in the Cellular Model[a]

Percentage of water partitioned in each direction from source cell	Tessellation vegetation cover fraction after 25 model iterations: Partitioning among six neighboring cells	Tessellation vegetation cover fraction after 25 model iterations: Partitioning among three neighboring cells
15%	0.238 (0.008)	0.266 (0.010)
10%	0.178 (0.002)	0.188 (0.004)
7.5%	0.136 (0.006)	0.156 (0.001)
5%	0.132 (0.002)	0.133 (0.002)

[a] *Note:* each vegetation cover fraction is the mean of five model runs in which the initial distribution of plants was varied at random. Standard deviations are noted in parentheses after the mean.

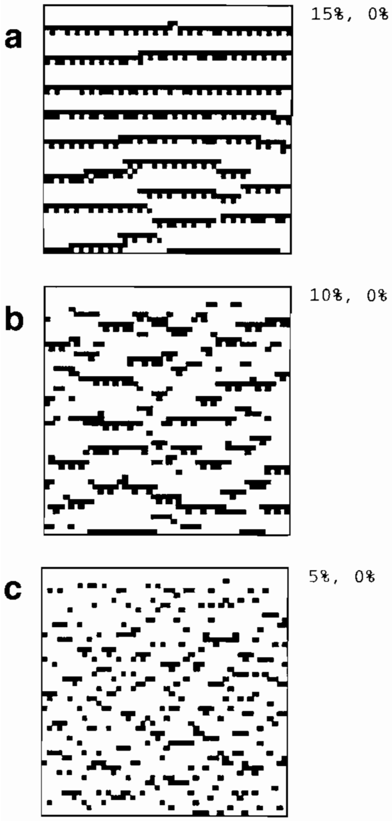


Figure 9.2. Instances of modeled band development with different water partitioning among three neighboring cells. The nearest neighbor partition coefficients are (a) 15%, (b) 7.5%, and (c) 5% (see text for detailed explanation).

Differences between plant cover arising as the quantity of water partitioned was reduced from 15% to 5%, for a given neighborhood size, were all statistically significant at the 1% probability level when tested by using a *t*-test for differences among means.

The conclusion to be drawn from these trials is that the model is sensitive to the amount of water partitioned among the neighboring cells and to the extent of water sharing (six cells or three). Variation in the amount of water partitioned results in far larger effects on plant cover than variation in neighborhood size. Thus, for example, increasing the amount of water partitioned in each direction from 5% to 15% increases the vegetation cover by 80% for a six-cell neighborhood and by 100% for a three-cell neighborhood, whereas changing the partitioning from six cells to three only increases the vegetation cover by 2.8% for 15% water sharing and 0.1% for 5% sharing. If the amount partitioned does not increase the soil wetness of adjacent cells sufficiently, plants do not develop there and the water is lost by evaporation. Patches of plants are then not linked to form bands. This emphasizes the importance of the spatial organization of plants in achieving concentration of water that can be exploited by the vegetation. This, of course, is fundamental to the operation of banded landscapes: they achieve the spatial concentration of limited available moisture so that it can then support plant growth in a way that would be impossible were the rainfall simply absorbed uniformly across the landscape. It should be emphasized that the particular values generated in the model are determined by the rules for plant colonization and removal embodied within it and do not relate to any particular species or plant community. Rather, the model points to conclusions that may have general applicability.

Varying the Infiltration Properties of Vegetated Cells. In the case of the banded vegetation in mixed grassland-shrubland investigated by Dunkerley and Brown (1999), there seems little prospect of runoff water emerging from the boundaries of a single runoff-runon unit. Runoff appears likely to be captured with high efficiency in the vegetated bands because of several characteristics of the ground surface there. The soils are relatively friable because of the higher organic matter content. They are also relatively porous owing to the effects of the soil fauna. Plant canopy cover protects the regolith surface to some extent, inhibiting seal and crust development. Finally, the surface has high microtopographic roughness, and scattered depressions produced by shrink/swell phenomena arising in subsoil smectites provide basins into which any moving surface water will gravitate. Surface runoff would also be obstructed by relatively abundant leaf litter on the ground surface.

In other areas, these features may not all be present or may be restricted in their development. Severe drought, for example, may reduce the contrast between band and interband to some extent. Shrub communities may generate lower surface litter abundance than grassland, so affecting the abundance of surface litter dams that serve to retard and pond surface runoff and so promote infiltration among plants.

Consequently, the cellular model has been run under conditions of diminished water-trapping efficiency in vegetated cells. Trials were run for the original value of 100% trap efficiency, together with lower values of 90%, 80%, and 70% trap efficiency. These percentages refer to the fraction of water moving onto the cell (from rainfall and runon) that is held within the cell. The remainder is passed downslope as runoff.

Within the model, sharing of water among adjacent cells laterally and downslope is maintained, even while the infiltration trap efficiency was varied. That is, when trap efficiency was reduced from 100% to 80%, 45% of the trapped water was still partitioned to the adjacent cells.

These trials indicate that banded patterns evolve strongly even when water retention is less than the complete absorption initially modeled. Some typical results are shown in Figure 9.3.

The major effect of reducing the water-trapping efficiency is to permit a larger fraction of the water arriving at a vegetated cell to pass on downslope. Thus, vegetated cells within the band receive more water through the upslope border of the band, and in turn, they are required to pass some of this downslope. Consequently, in the model the vegetated bands become wider in the downslope direction. Bandwidths are about two, three, or four cells with 90%, 80%, or 70% water absorption, respectively. Generally, the upslope margin of the bands is sharp, and the

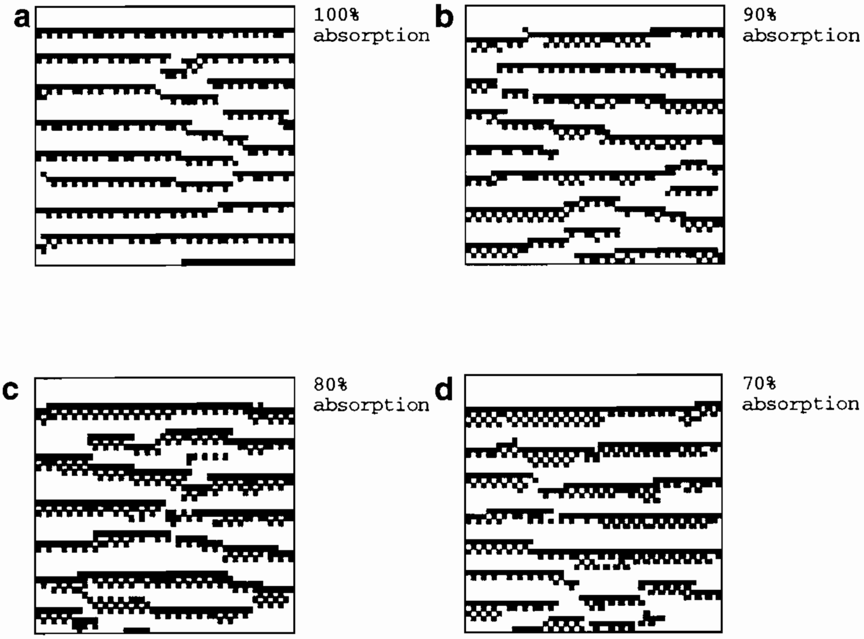


Figure 9.3. Instances of modeled band development with different water absorption in vegetated cells. The water absorption coefficients are (a) 100%, (b) 90%, and (c) 70% (see text for detailed explanation).

downslope parts are somewhat more diffuse, with unvegetated and vegetated cells mixed. This is in accord with field observations in Niger (Couteron et al. 2000).

The vegetation cover fractions obtained for different water absorption (with different runs and different random initial distributions) are not significantly different at the 1% probability level. Thus, in contrast to the finding presented above for the amount of water shared among neighboring cells, varying the water-trapping efficiency in a vegetated cell does not markedly affect the final plant cover. However, this parameter does evidently influence the spatial structure of the banding. Bands appear wider and display more variation in plant density, when the trapping efficiency is lowered. Again, this seems intuitively reasonable, because more water is able to pass into the grove. The fact that banding is strongly developed in all cases tested confirms that the cellular model is not strongly sensitive to the level of water trapping assumed.

Variable Annual Rainfall. Five periods of 25 years with log-normally distributed varying rainfall were simulated. In all runs, water trapping in vegetated cells was set at 100%, and 15% of water was partitioned in each direction among six neighboring cells. In all runs with variable rainfall, vegetation banding evolved. The level of plant cover across the tessellation of cells fluctuated significantly more between iterations than in constant rainfall runs. Bands became wider in wet iterations and narrowed when the rainfall was low.

The mean rainfall generated in the five runs of 25 years was 112 mm. This is close to the fixed value of 100 mm used in previous simulations. The overall mean vegetation cover from the same five runs with varying rainfall was 0.227, which is not significantly different (at the 1% level) from the value 0.238 reported in Table 9.1. Clearly, in this model, year-to-year rainfall fluctuations such as those experienced by the plant communities of western New South Wales do not inhibit the development of banding nor affect the long-term plant cover.

A statistically significant ($p = .02$) linear relation exists between the vegetation plant cover and the mean rainfall:

$$\text{veg. cover fraction} = -0.026 + 0.002 * (\text{mean rainfall in mm})$$

The coefficient of determination (r^2) is 0.87, and the standard error of estimate 0.008.

Typical arrangements of the vegetation cover during a variable rainfall run are shown in Figure 9.4.

In these diagrams, it is evident that the band dimensions vary as a function of the sequence of varying rainfall. In particular, the vegetation bands become wider in years of above-average rainfall and narrower in dry years. In wet years, more water evidently passes into and through the band to enable and support plant growth beyond the normal downslope margin of the band. In dry years, plants here no longer receive sufficient moisture to survive, and the lower band margin retreats upslope. This appears to provide an alternative explanation for the evidence of former plant growth downslope of vegetation bands. In terms of the model used here, it seems possible for this to reflect the recent history of site rainfall. However, elsewhere the same evidence has been taken to indicate active upslope migration of the whole vegetation band, rather than just the downslope border. Mougenot, d'Herbès, and Ichaou (1996) argued this, for example, for sites in Niger. Contrasting results were reported from the Chihuahuan Desert of Mexico, where a vegetation band was monitored for several years by Cornet, Delhoume, and Montaña (1988). They recorded upslope expansion during wet years but did not observe clear regression of the lower margin. Some gaps in the lower grove were noted, resulting from the death of tufts of the grass *Hilaria mutica*. More instances of field monitoring of band width and of colonization or regression mechanisms at the upslope and downslope margins are clearly necessary for general conclusions to be drawn about the circumstances under which such events take place.

Discussion of the RUNONOFF Model

The results presented above are based on a simple cellular model. This, however, seems an appropriate modeling tool, because it permits encapsulation of the essential features of vegetation bands and their hydrological functioning. The model removes the need for a high level of process knowledge. For instance, actual infil-

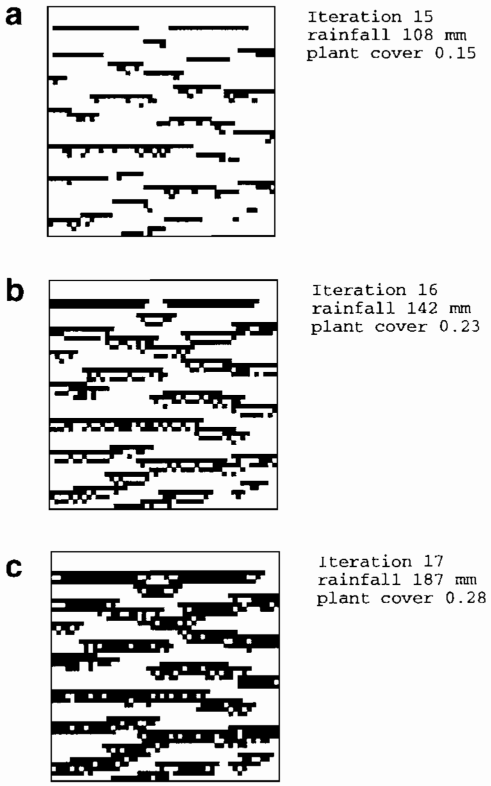


Figure 9.4. Plant distribution for three successive iterations in a model run with log-normally distributed varying annual rainfall. Rainfalls were (a) 108 mm, (b) 142 mm, and (c) 187 mm. Plant covers were (a) 0.15, (b) 0.23, and (c) 0.28 (see text for detailed explanation).

tration capacities of band and interband soils need not be known. Rather, the model is built on the condition, always clearly evident in the field, and reflected by the plant distribution that infiltration is greater and promotes higher levels of available soil moisture within plant bands than within intergroves. On the condition that this contrast in infiltration is embodied within the model, the model may be said to represent a key feature of reality simply, but seemingly adequately, for the level of investigation undertaken here. No data on the detailed reasons for the contrast in infiltration behavior, many of which are known in outline, are required within the model. But were "pioneer" zones predicted? These have been widely observed empirically. If not, this remains an area in which the model can be modified.

Nevertheless, there remains considerable scope for the incorporation of more "calibration" data tied to measurements made in real banded landscapes. The potential significance of canopy interception losses of rainfall within the banded landscapes of western New South Wales has recently been examined in this context (Dunkerley and Booth 1999). In this work, it was shown that in banded communities of Mitchell (*Astrebla*) grass, canopy interception losses amount to approximately 30% of the annual rainfall, largely offsetting the benefits of the runon water arriving from unvegetated bands upslope, that has been estimated at 40% of the annual rainfall. These are annual aggregate figures, and further work would be required to resolve whether there are nonetheless larger beneficial increments of runon water in the bigger storm events, during which the depth of water delivered to the landscape could greatly exceed the capacity of the canopy interception store and so supply water to the soil supporting the grassy vegetation.

Other remarks on this model apply to all cellular models and are developed in the final discussion.

Conclusion on the RUNONOFF Model

Despite its simplicity, the RUNONOFF model provides a useful means of testing certain ideas about the evolution of banded vegetation mosaics. In particular, the following conclusions arise from the present work and from earlier studies:

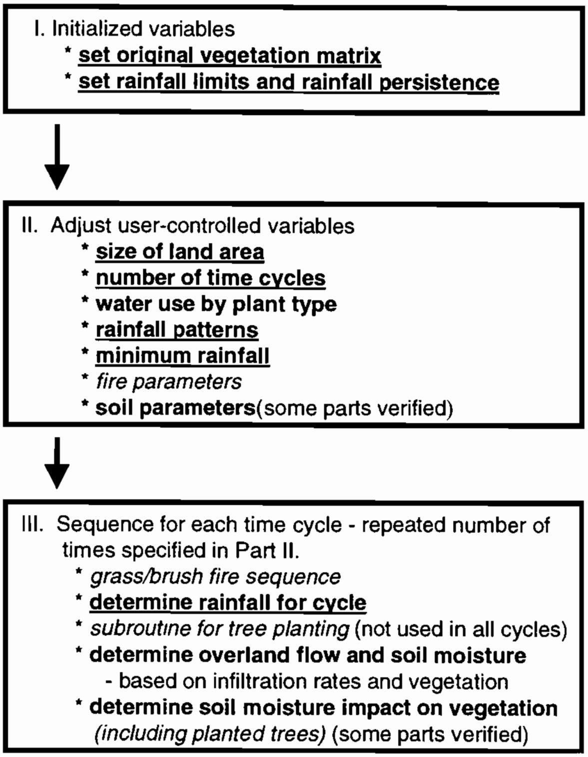
1. Neither climatic deterioration nor drought is necessary conditions for the development of vegetation banding. Rather, this can arise even under rainfall that is absolutely uniform from year to year.
2. The spatial extent and volume of across-slope partitioning of absorbed water seems to be critical to the spatial extent of vegetation bands. The dominant influence arises from the amount of water partitioned laterally. Limited cross-slope water movement yields short separated band fragments; as the amount of lateral water movement is increased, so too does the length of the resulting bands.
3. Water infiltration in the vegetated band must be greater than that in interbands, but banding appears in the model for a significant range of infiltration characteristics.
4. Interannual variability in rainfall, at least of the kind experienced in western New South Wales, does not inhibit the development of banding. This is clear both from the model results and from the occurrence of banded vegetation in this region. The model suggests that over a period of years, a banded site experiencing fluctuating annual rainfall can maintain the same average plant cover as one experiencing reliable rainfall.
5. Bands may widen in the upslope-downslope direction in years of unusual wetness. The lower band margin, in particular, seems to advance downslope when additional water is passed through a band. The area thus colonized appears to be abandoned when rainfall declines. The resulting upslope retreat of the band margin does not, however, imply the upslope migration of the entire vegetation band. This point is developed in the general conclusion.

TGRBR Model

The model TGRBR (Orr 1996) was developed to investigate three primary questions among those already presented in the general introduction. First, how does *brousse tigrée* form, and specifically, can it form from a random pattern of vegetation submitted to decreasing rainfall? Second, do vegetation bands move uphill? Finally, what are the management implications? Especially, what happens if one plants vegetation in the bare parts of the bands? If the bare bands are necessary for the survival of the plants in the vegetation bands, will planting disrupt a key ecosystem process and lead to a net loss of biomass (Orr 1995)?

TGRBR is a simulation model programmed in C++ (Borland C++ v. 3.1) (Orr 1996) and is still under development. An outline of the model is shown in Figure 9.5. The model has three general functional areas.

Part I, the first functional portion of the program, establishes a matrix that represents a landscape. All points in a given row in the matrix are assumed to be at equal elevation, with the top of the matrix (the lower numbered row in the C++ array) as the highest elevation. The program randomly fills the matrix (landscape) with symbols representing trees, grasses, and bare ground, although density and relative proportions of each plant type are controlled by the user. Herbaceous vegetation plays an important role in some *brousses tigrées* (e.g., in northern Burkina



I. Initialized variables
- **set original vegetation matrix**
- **set rainfall limits and rainfall persistence**

II. Adjust user-controlled variables
- **size of land area**
- **number of time cycles**
- **water use by plant type**
- **rainfall patterns**
- **minimum rainfall**
- *fire parameters*
- **soil parameters**(some parts verified)

III. Sequence for each time cycle - repeated number of times specified in Part II.
- *grass/brush fire sequence*
- **determine rainfall for cycle**
- *subroutine for tree planting* (not used in all cycles)
- **determine overland flow and soil moisture**
  - based on infiltration rates and vegetation
- **determine soil moisture impact on vegetation** *(including planted trees)* (some parts verified)

Figure 9.5. General scheme for one run of the model TGRBR. Not all details are shown. Bold and underlined portions are complete and verified; bold portions are complete but not yet verified; italics portions are incomplete.

Faso [Couteron 1998] and in western New South Wales [Tongway and Ludwig 1990] and a lesser one in Niger). There is no differentiation among tree species or ages; all trees are identical species and age, although they may be under different levels of moisture stress. Rainfall patterns, including the ability to program long-term declining rainfall, following Nicholson (1978), and rainfall persistence, following Dunne and Leopold (1978), are also controlled by the user.

Part II of the program controls additional model parameters defined by the user. Within the program, limits are placed on the range each variable may have to mimic rainfall in the Sahel. The goal of program-defined limits is to keep user-defined changes within boundaries that will duplicate overland flow and water-use patterns described for *brousse tigrée* and, more generally, other mosaic vegetation types (White 1970; Ambouta 1984; Mauchamp et al. 1993).

Part III of the model, at its current stage of development, allows rain to fall on the landscape and flow overland until it reaches permeable soil. Infiltration is driven by nearby vegetation. It is interesting to note that the infiltration pattern for trees in TGRBR (Figure 9.6) is similar to the interaction matrix of the model TIGREE (Thiéry, d'Herbès, and Valentin 1995). Thus, plants "help each other to survive" by the amelioration of soil crusts. Competition results from the scarcity of water, and it is assumed in the model construction that uphill trees in each vegetation band have greater access to the water through infiltration. Plants then survive, decline, or die based on the available water. The user also determines the number of time cycles that the model will run in part III of the program. The model is designed for expansion into other semiarid landscapes, and some features of the model, such as fire, are less important when modeling *brousse tigrée.*

Three matrices from a typical run of the model are shown in Figure 9.7a to c. Figure 9.7a shows the initial condition of the vegetation array, a randomly generated landscape. It is assumed that vegetation is denser than in *brousse tigrée* as several studies indicate this is a distinct possibility given the long-term precipitation trends in the Sahel and Sahara (Ambroggi 1966; Nicholson 1978). Figure 9.7b shows the vegetation array two cycles into the pattern. Note that most of the scattered vegetation is under stress, it was too dense for the available rainfall, and some bands are forming. One key problem with the current model is that the bands in the early part of a simulation are typically only one unit of vegetation thick. The subroutine that will allow trees to recover their health in high rainfall years and linking moisture infiltration to vegetation should overcome this limitation. This is still under development. Figure 9.7c shows the landscape after 22 cycles. This current wet cycle was preceded by three wet cycles and two dry cycles. The model uses integers to represent 15 different rainfall levels. "Wet" cycles are those that

1	1	1	
2	4	2	↑
4	4	4	uphill
4	10	4	↑

Figure 9.6. Soil moisture infiltration indices. Location marked by the value 10 is the location of the tree.

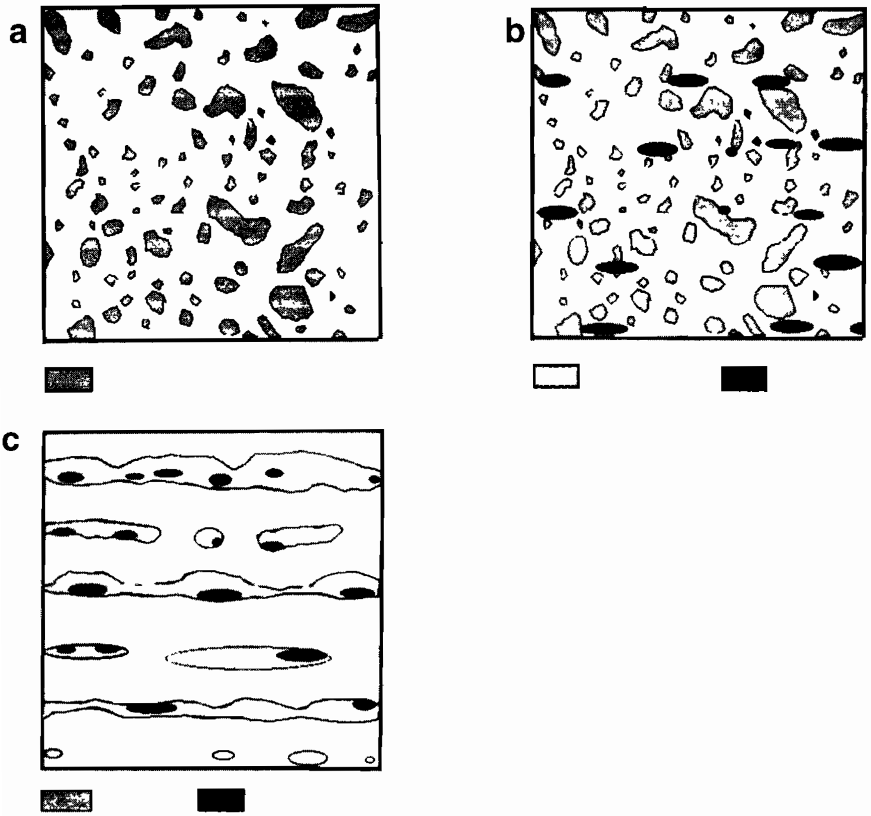


Figure 9.7. Evolution of the vegetation map: (a) initial vegetation, (b) evolution after one cycle of dry weather followed by one cycle of wetter weather, (c) evolution after 22 cycles (the current wet cycle was preceded by three wet cycles followed by two dry cycles). Gray (only in a and b), black (only in b), gray (only in c), and black (only in c) areas represent, respectively, initial vegetation, incipient banded vegetation, sparser vegetation, and denser vegetation.

have sufficient rainfall to allow runoff between bands to generate adequate water for trees to avoid moisture stress during the rainy season. Here, the vegetation bands are more than one unit thick, and the gaps in the bands typically found in *brousse tigrée* are present.

The model, if an accurate representation of physical processes, clearly shows that bands do form based on topography and climate. Band movement is also evident, although erratic. It does not show the smoother changes implied by Ambouta (1984). The model itself does not yet allow drought-stressed trees to recover in better years. This may smooth out band transformation and generate some of the irregularities and discontinuities that are common in the vegetated portion of the banded pattern. Finally, the third question, "Is tree planting in bare bands a wise management practice?" cannot be determined until the tree planting subroutine is operational. However, because most tree planting uses water catchment methods that disturb the soil surface, these techniques will dramatically alter water capture by what is currently bare ground with limited infiltration between vegetation bands (Heermans and Minnick 1987). Water that infiltrates in the microcatchments constructed for tree planting will no longer be available to natural vegetation in the bands.

LEJEUNE-LEFEVER Model

The preceding models were based on cellular automata. This formalism is well adapted to the numerical simulations of experimental data, which can be represented by landscape matrices (e.g., within a raster geographical information system). Some intrinsic parameters of cellular automata (e.g., the dimensions of the interaction matrix) are discrete, which precludes the study of intermediate cases. To make systematic predictions from analytical results, it is interesting to introduce continuous models in which all parameters may be finely studied, especially near critical values. One continuous model of banded vegetation was developed several years ago (Lejeune and Lefever 1996) and another one more recently (Klausmeier 1999).

The LEJEUNE-LEFEVER Π model (where Π stands for "propagation-inhibition") describes the dynamics of banded vegetation growing in arid or semiarid regions throughout the world. The following paragraphs summarize different aspects of this model described in recent publications (Lefever and Lejeune 1997; Couteron 1998; Lefever, Lejeune, and Couteron 1998; Lejeune, Couteron, and Lefever 1999; Lejeune and Tlidi 1999).

This model introduces a "transport process by reproduction" that is specific to biology (because it does not conserve the mass) and especially to botany (because plants cannot propagate without reproduction).

The emergence of a periodic pattern results from the interplay between short-range cooperative (or facilitative) interactions controlling plant reproduction and long-range self-inhibitory interactions originating from plant competition for environmental resources. The model introduces a common framework for the discussion of isotropic as well as anisotropic environmental conditions.

In isotropic conditions (e.g., on homogeneous flat terrains), the model predicts different types of patterns depending on the values of critical parameters: parallel bands, zigzag bands, or hexagons. The general directions of these patterns depend on the initial conditions. Spatial defects in pattern shapes may appear when simulations are run on large-size systems.

In anisotropic conditions (e.g., on a regular slope), vegetation bands tend to orient themselves in the direction parallel or perpendicular to the anisotropy direction. If the reproduction is anisotropic, then bands are parallel to the anisotropy direction and their position is stationary. If the inhibition is anisotropic, then bands are perpendicular to the anisotropy direction and move upslope (under specific conditions, these bands may be changed into arcuate patterns). In all cases, the wavelength of the vegetation bands increases when environmental conditions get more arid.

An important necessary condition for the formation of periodic vegetation patterns is that the spatial range characterizing the cooperative plant reproduction must be shorter than the one associated with self-inhibition.

A first attempt at calibrating the model has been performed with the Fourier transform of a digitized aerial picture of a *brousse tigrée* in Burkina Faso. With the actual crown and root diameters, the mean band wavelength might be explained by a high cooperativity in plant reproduction.

KLAUSMEIER Model

The KLAUSMEIER model (1999) is a simple model of plant and water dynamics based on ecologically realistic assumptions. This model is a continuous spatial model defined by two partial differential equations (one first order and the other second order).

As in the LEJEUNE-LEFEVER model, regular patterns appear on sloping plateaus. In the long term, vegetation bands are perpendicular to the slope and move uphill. Band defects in the form of forks and dead-ends appear during the transient dynamics. The wavelength of the regular patterns increases with decreasing water input.

Contrary to the LEJEUNE-LEFEVER model, linear stability analysis shows that regular pattern formation is impossible on flat ground. A potential explanation for the irregular mosaics is that slight topographic variation can lead to large variation in plant density.

This model provides a clear example of how nonlinear mechanisms can be important in determining the spatial structure of plant communities.

Conclusion

Models presented in the previous sections are based on different assumptions and are written with different formalisms. But they also have some common features imposed by the main characteristics of banded vegetation. Differences and similarities are displayed on Table 9.2.

The previous models work on similar space and time scales, so that they can normally be tested with the same experimental data sets. Presently, their quantitative comparison and validation are hindered by the lack of long-term field measurement under controlled conditions. For example, in Niger, aerial photographs have been recorded for about 40 years but for other purposes. Moreover, many *brousses tigrées* have been degraded by severe droughts and by an increasing anthropic pressure. Wu, Thurow, and Whisenant (2000) have recently used aerial photographs to assess landscape degradation over the period 1960 to 1991.

Most models summarized in Table 9.2 predict an upslope migration of vegetated bands. This migration may be slow for some parameter values of the TIGREE model or negligible for the TIGRFLUX or RUNONOFF models. Experimental data on upslope migration would be important for the choice of the best model, after proper calibration.

The level of abstraction represented by these models has considerable use. Their intrinsic simplicity also creates extensive limitations to the uses to which the model may be put. Some examples will serve to illustrate this.

Most cellular automata introduce no explicit reproduction equation. They implicitly assume that reproduction is not a limiting factor and that favorable cells are rapidly colonized by plants. Plant growth is implicitly taken into account by the transition rules from one state to another one at each iteration.

No erosional processes are as yet incorporated in these models. Therefore, these models are insensitive to potentially significant changes that might arise in a real landscape. Parts of the tessellation that become bare in low rainfall years might prove prone to channel initiation in a following wetter-than-average year or in response to some anthropic disturbance. The risk of this occurring is enhanced as the upslope-downslope extent of any bare area increases and as the rainfall following the dry spell increases. On long bare patches, sufficiently large amounts of surface runoff might accumulate to generate shear stresses able to carry away the surface regolith. Rills so generated would disrupt the surface hydrology of the mosaic and provide pathways for rapid water loss. Many models, especially those that incorporate high levels of ecological knowledge, suffer from deficiencies such as this. They are difficult to overcome, because adequate knowledge of field conditions and shear processes in surface runoff are not developed enough.

The coarse time-steps of the cellular models, in which each iteration is taken loosely to represent 1 year or several years, prohibit finer scales of temporal analysis. For example, these models incorporate no data on detailed rates of plant growth or on particular types of rainfall events, which precludes any seasonal analysis (chapter 8, this volume).

Conversely, most of the preceding landscape models depend on a small number of parameters, which simplifies stability analyses. After proper calibration and far from critical conditions, these models should predict robust and safe management rules.

From a forest manager's perspective, the true value in using the preceding models is twofold. First, these models allow one to understand the ecological process in the woodland. Good forest management works with ecological processes, not against them. Second, models can allow a land manager to simulate changes such as tree planting between vegetation bands (Thiéry, d'Herbès, and Valentin 1997). If, as most researchers believe, bare ground is a key component of *brousse tigrée* then tree planting is, at best, a futile activity in these areas.

From an ecologist's perspective "brousse tigrée" is an important ecosystem to understand. As the peculiarities of slope and rainfall combine to form an evident vegetation pattern, modelers can isolate key hydrological factors interacting with vegetation. The model can then be expanded to investigate other aspects of *brousse tigrée,* such as nutrient cycling. It could also be generalized for other ecosystems

Table 9.2. Comparison of Five Landscape Models for Banded Vegetation[a]

	DISCRETE MODELS			CONTINUOUS MODELS		
Model names	TGREE [*E*] TIGRFLUX [*F*]	RUNONOFF	TGRBR	LEJEUNE-LEFEVER	KLAUSMEIER	Model names
Formalism	Cellular automata	Cellular automata	Cellular automata	Integrodifferental equation and 4th order partial equation	2nd order partial differential equations	Formalism
Observable(s)	Biomass Water [*F*]	Biomass	Biomass	Biomass	Biomass Water	Observable(s)
Number of states	4 [0, 1, 2, 3]	2 [0, 1]	3 [0, 1, 2]	0 ≤ density ≤ ~K	0 ≤ density 0 ≤ water	Variation range
Phenomena directly taken into account	Biomass growth Biomass loss Precipitation [*F*] Runon [*F*] Evaporation [*F*] Water storage [*F*]	Biomass growth Biomass death Precipitation Runon Partition	Biomass growth Biomass loss Precipitation Runon Infiltration	Biomass growth Biomass death Plant dispersal	Biomass growth Biomass loss Plant dispersal Precipitation Runon Evaporation Water storage	Phenomena directly taken into account
Non limiting phenomena	Plant dispersal	Plant dispersal	Plant dispersal			
Global parameters	Synergy Competition [*E*]	Synergy	Propagation Inhibition			Global functions
Normalized time or time unit	Iteration—5 years	Iteration—1 year	Iteration—5 years	Reproduction cycle period	Normalized time *t*	Normalized time or time unit

Normalized parameters	Lateral synergy b Competition $a[E]$			Cooperativity Λ Aridity μ	Plant loss m Water input a Water velocity v	Normalized parameters
Main results in isotropic environment	Bare spots, maze patterns, or vegetated spots for near-isotropic			Bare hexagons, bands, zigzags, or vegetated hexagons	No regular pattern High sensitivity to topographic variation	Main results in isotropic environment
Main results in anisotropic environment	Bands orthogonal to the anisotropy direction and moving uphill, for anisotropic competition	Bands orthogonal to the anisotropy direction	Bands orthogonal to the anisotropy direction and moving uphill	Bands orthogonal to the anisotropy direction and moving uphill, for anisotropic inhibition Stationary bands parallel to the anisotropy direction, for anisotropic cooperation	Bands orthogonal to the anisotropy direction and moving uphill	Main results in anisotropic environment
Interaction range	Short-range synergy and long-range competition			Short-range cooperation and long-range inhibition		Interaction range
				Band wavelength increases with aridity	Band wavelength increases with decreasing water input	Other result

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[a] In column 2, E and F refer to the TIGREE and TIGRFLUX models, respectively, see text for other comments.

where slope is not important but where fire, more complex competition, and seed dispersal mechanisms play an important role in landscape organization.

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10. Productivity of Patterned Vegetation

David O. Freudenberger and Pierre Hiernaux

Introduction

In the course of this book, the patterning of banded vegetation has been described at various scales (chapters 1 and 4), a theory of its genesis has been proposed (chapters 2 and 3), and many of the internal processes of patterns have been summarized (chapters 5 and 11).

This chapter examines the importance of the banding pattern of vegetation on plant and herbivore productivity in semiarid and arid landscapes. Banding is a striking indicator of concentration of scarce resources of water and nutrients. This concentration has a strong influence on productivity. This redistribution of resources increases temporal and spatial variation in productivity.

The spatial and temporal concentrations of primary productivity are important to human economies that have participated in these landscapes for centuries either directly through clearing for crops or consumption of firewood and timber or indirectly through grazing of livestock. Banded landscapes are reasonably resilient to use; however, overcultivation and overconsumption can lead to a loss in the capacity of bands to capture scarce resources such as runoff, which results in long-term losses in plant and animal productivity.

The processes that create and maintain banded vegetation patterns are critical to plant and herbivore productivity. If patterning is lost through overclearing and overconsumption, the responsiveness of the system to rainfall is severely impaired.

Noble and co-workers (chapter 11, this volume), focus on management of banded landscapes.

Primary Productivity

Primary productivity is clearly concentrated within patches or bands. Runoff slopes between patches are often completely devoid of vegetation in both African and Australian banded landscapes (Wickens and Collier 1971; Mabbutt and Fanning 1987). By contrast, the plant biomass within a band can be remarkably high. For example, there were 53.8 t ha^{-1} of wood in the groves and only 0.6 t ha^{-1} in the intergrove of a *brousse tigrée* site in southwestern Niger. These tonnages corresponded to 4519 stems ha^{-1} in the grove and 151 stems ha^{-1} in the intergrove (Hiernaux and Gérard 1999). Density of mulga trees (*Acacia aneura*) in patterned groves in semiarid woodlands in eastern Australia can be 4000 stems ha^{-1} (Pressland 1976).

Similarly, herbage yield was 105 times greater at the upslope edge of a band compared with the runoff slopes between bands at various *brousse-tigrée* sites in the Sahel (Table 10.1). In the southern Sahel of Niger, the herbage layer is dominated by ephemeral species of grasses, legumes, and other dicots, with a growing period of 60 to 100 days during the annual wet season with an annual yield of 500 to 1200 kg dry matter (DM) ha^{-1} depending on rainfall (Achard 1993). A similar yield of herbaceous vegetation has been reported for other regions of Niger and Burkina Faso (Geerling and De Bie 1988; Chase and Boudouresque 1989; De Winter et al. 1989).

In contrast to *brousse tigrée*, the banding of vegetation is generally less pronounced in the semiarid woodlands of Australia, and the differences in productivity between runoff slopes and runon bands are less pronounced. For example, within a patterned mulga woodland in eastern Australia, herbage yield was on average only 4.5 times as great at the upslope edge of the bands compared with the runoff slopes (see Table 10.1). However, the proportion of herbage production in the various zones depends on the intensity of rainfall. Noble, Greene, and Müller (1998) reported a substantially greater proportion of herbage production in the upslope edge of the band after an intense rainfall with considerable runoff, compared with a small rainfall event with little runoff (Table 10.2).

Productivity in a band can be markedly different to a similar band elsewhere along an elevational catena. Studies in a banded mulga (*A. aneura*) community in central Australia found that herbage yield was greatest (9.6 kg DM ha^{-1} mm $rainfall^{-1}$) in the sparsely timbered groves of the upper slopes where considerable runoff was generated from the intergrove zone. In the lowest and more densely timbered groves, herbage yield was only 0.1 kg DM mm $rainfall^{-1}$ (Lendon and Ross 1978).

Plant productivity also varies within bands or groves. Mean herbage yield was greatest in bands of grass immediately upslope from the margin of trees in both the Sahelian and Australian studies (see Table 10.1). Distinctive grassy bands upslope from trees or shrubs have been noted in other African and Australian land-

Table 10.1. Mean Herbage Yield (kg DM/ha^{-1}) from Three Landscape Zones in Banded Woodlands in the Sahel[a] and in Eastern Australia[b]

	Runoff slope	Upslope edge of band	Core of band
Sahel	25	2618	430
Eastern Australia	220	997	640

[a] From Hiernaux and Gérard (1999).
[b] From Freudenberger and Palmer (unpublished data).

scapes (Worrall 1960; Boaler and Hodge 1964; Hemming 1965; Boyland 1973; Mabbutt and Fanning 1987). The species composition of the vegetation, density, size, and age of plants also vary within the grove (López-Portillo and Montaña 1999; Valetin and d'Herbès 1999). In the Sahel *brousse tigrée*, linear relationships have been established for the main woody species *Guiera senegalensis* and *Combretum micranthum* between the age of individuals and the distance that separates them from the upslope edge of the grove (Ichaou and d'Herbès 1997). These relationships were used by the authors to assess the speed of the upslope progression of the grove as 0.5 m per year.

Plant productivity within and between bands is a function of rainfall (Noble, Greene, and Müller 1998) but also area of runoff slope compared with area of runon. In the West African Sahel, studies of Hiernaux and Gérard (1999) found that the ratio of runoff to runon areas varied between 10:1 and 1:1. Along a climatic gradient in western Niger, studies by Valentin and d'Herbès (1999) found that ratio varied between 0.5 and 2.5 in a negative exponential relation with the average annual rainfall. The width of the pattern period (grove + intergrove) decreased with steeper slopes (d'Herbès, Valentin, and Thiéry 1997). Increasing aridity generally corresponded to an increase in the proportion of runoff area. In the Sudan, the ratio varied between 4.7:1 and 0.9:1 (Worrall 1959, 1960). In Australia, within a patterned mulga woodland described by Tongway and Ludwig (1990) the ratio was also approximately 1:1 (D. Freudenberger, unpublished data). The semi-arid woodlands of Australia are generally more diffuse; that is, banding is less pronounced. However, Boyland (1973) reported that a banded pattern was more distinct in more arid regions of eastern Australia.

Much of the spatial variation in primary production in banded landscapes is due to the redistribution of rainfall via surface runoff. If the runoff into a band is pre-

Table 10.2. Total Herbage Production (kg DM/ha^{-1}) in Three Landscapes Zones 4 Weeks following Minor and Major Rainfall Events in an *Acacia aneura* Woodland in Eastern Australia[a]

	Runoff slope	Upslope edge of band	Core of band
16-mm rainfall event	7	29	15
43-mm rainfall event	3	124	65

[a] From Noble, Greene, and Muller (1998)

vented by experimental manipulation, herbage yield is depressed. When incident rainfall was impounded within the runoff slope of an *Acacia aneura* woodland, the standing yield of *Thyridolepis mitchelliana,* a perennial grass found in the core and upslope edge of bands in eastern Australia, was more than 2.5 times less than in the control plots where runoff was unimpaired. Conversely, the impounded water increased the yield of the grass *Eragrostis eriopoda* by a factor of 2.5 within the runoff slope (Noble, Greene, and Müller 1998). A similar study was conducted in a *brousse tigrée* landscape in southwestern Niger (Seghieri and Galle 1999). A low wall constructed upslope of a band significantly reduced the within-band density of *Cyanotis lanata,* the subdominant herbaceous species in this landscape. The reduction in plant production was related to the lowering of soil moisture storage and shallower depth of infiltration in all the zones of the band deprived of runon compared with the control band (Seghieri and Galle 1999).

Woody vegetation appears to be greatly advantaged in banded landscapes compared with diffuse landscapes. In neighboring patterned and diffuse sites, Ichaou and d'Herbès (1997) and Hiernaux and Gérard (1999) found that the herbaceous production and the density of woody plants were superior in diffuse landscape, whereas the average standing woody biomass was superior in the patterned. Another study examined the water harvesting potential in terms of crust character in patterned landscapes and compared the production to that of diffuse landscapes that received the same rainfall (Valentin and d'Herbès 1999). This showed a large and systematic superiority in standing wood mass per hectare for the banded landscape in the 300- to 600-mm rainfall range, compared with diffuse landscapes.

Although the primacy of differential water supply in the band and interband in controlling productivity is acknowledged, the concomitant role of nutrients cannot be ignored. In Australia (Tongway and Ludwig 1990) and in Niger (Guillaume et al. 1999), much larger organic nutrient pools exist in the vegetated bands compared with the interband, as a consequence of effective organic matter cycling over time. By implication, when runon water flows into the band, there will be a large flush of mineralized nutrients to support plant growth, especially perennials that have the capacity to take up nutrients in large amounts soon after rain, compared with annuals that need to germinate from seed. The role of perennial plants in improving their local edaphic environment was predicted in outline by Tongway (1990) and confirmed by Ludwig and Tongway (1997).

The species composition of the vegetation and density, size, and age of the plants also vary within the grove (López-Portillo and Montaña 1999; Valentin and d'Herbès 1999). In the Sahel *brousse tigrée,* a linear relationship has been established for the main woody species *Guiera senegalensis* and *Combretum micranthum* between the age of individual plants and the distance that separate them from the upslope edge of the grove (Valentin and d'Herbès 1999). These relations were used to assess the speed of the upslope progression of the grove at 0.5 m yr^{-1}.

Temporal Variation of Production

Plant productivity is clearly patchy across banded landscapes, as well as highly variable through time. The coefficient of variation (CV) in annual herbage yield

(177 kg DM ha^{-1}) in *brousse tigrée* was 441% over ten years across a number of sites in the Gourma region of Mali (Hiernaux and Gérard 1999). Less variation in herbage yield has been reported in a more diffuse *Acacia* woodland in southwestern Queensland, Australia (Beale 1973; mean 753 kg DM ha^{-1}, 43.4 CV%).

This variation in plant productivity is due primarily to variation in rainfall, particularly its intensity and duration. The CV of mean annual rainfall is typically greater than 50% in many arid and semiarid rangelands (Le Houérou, Bingham, and Skerbek 1988; Ellis, Coughenour, and Swift 1993). However, annual averages are only one measure of variation in rainfall. The seasonality (e.g., warm vs. cool season) of rainfall may also be important. For example, in Australia summer rainfalls dominates in the northern half of the continent, winter rainfall dominates in the southern fringe, and there is no distinct seasonal pattern in a band across the lower third of the continent (AUSLIG 1992). The growth response (e.g., g DM mm $rainfall^{-1}$) to cool season rainfall is generally greater than for warm season rainfall because of the far greater potential evapotranspiration rate in the summer, assuming there is little runoff.

When rain does occur, most events can be small in banded landscapes in Australia. For instance, 65% of days with rain had total falls less than 5 mm, whereas only 8% of days with rain had falls greater than 20 mm in the semiarid woodlands near Cobar, Australia (calculated from Clewett et al. 1994).

Additional variation in herbage production in banded vegetation is probably due to the high variation in occurrence and intensity of runoff. The intensities of rainfall were on average fairly low, but maximum intensities of more than 100 mm h^{-1} were recorded over increasing lengths of time in an area of semiarid woodlands in eastern Australia (Table 10.3). Relatively rare rainfall events of long duration and high intensity are probably the key processes that shape landscape structure at least in the nonseasonal semiarid woodlands of eastern Australia.

When there is sufficient soil water, short-term growth rates of herbage within patterned woodlands can be high. A maximum growth rate of 27 kg ha^{-1} d^{-1} was reported for herbage production from primarily perennial grass (*Thyridolepis mitchelliana, Monachather paradoxa, Themeda triandra*) in a mulga (*A. aneura*) woodland in eastern Australia (Christie 1978). In the same region, a maximum rate of 90 kg DM ha^{-1} d^{-1} were reported for an wooded grassland dominated by *Aristida* spp. (Pressland and Lehane 1980). These growth rates occurred soon after rainfall and quickly declined in the absence of further rain.

Table 10.3. Rainfall Intensities (mm h^{-1}) at Three Arbitrary Time Intervals at Cobar, New South Wales, in the Semiarid Woodlands Region of Eastern Australia[a]

	6 min		30 min		60 min	
	Mean	Max.	Mean	Max.	Mean	Max.
Warm season (Oct–Mar)	32	116	16	119	10	88
Cool Season (Apr–Sept)	17	94	9	31	5	28

[a] Data compiled by D. Tongway from Australian Meteorological Bureau records from 1963 to 1983 reported in Hodgkinson and Freudenberger (1997).

Hiernaux and Gérard (1999) hypothesized that the marked spatial heterogeneity of banded vegetation would buffer temporal variations in herbage yields. However, they found that temporal variation was consistently higher in banded vegetation than in more diffusely patterned landscapes nearby. Hiernaux (1995) found that temporal variability in herbage yield increased with spatial variability across a diversity of landscapes.

Uses of Banded Vegetation

Animal Production

Banded or patterned semiarid and arid landscapes are used for a variety of purposes. The mulga (*A. aneura*) woodlands of Queensland, Australia, supports approximately 2.5 million sheep (25% of the state's flock) and 4% of the state's cattle herd. The gross value of livestock production was $127 million for this region in 1988, representing 15% of the state's total value of livestock production (Anonymous 1993). Banded vegetation in Australia also supports millions of kangaroos (*Macropus* spp.) and hundreds of thousands feral goats (*Capra hircus*), both of which are commercially harvested (Ramsay 1994).

In southern Niger, the banded woodlands are a seasonally important source of fodder for livestock in the region (Achard 1997). From January to March (mid–dry season), they support transhumant herds from the northwestern region of the Niamey department. In addition, these woodlands are grazed from July to April by local herds of cattle, sheep, and goats. At other times, local livestock forage off of crop residues and fallowed fields. Over an annual cycle, these woodlands provide two-thirds of the fodder resources for the villages in the region (Achard 1997). In the Tientiergou region (30,000 ha) of southern Niger, surveys during the mid-1990s showed that 20,000 head of cattle and 25,000 small ruminants grazed continuously in the area, and 10,000 cattle and 18,000 small ruminants grazed for a 2-month period during regular transhumant movements (Peltier, Lawali, and Montagne 1994).

Quality of Primary Production

The grazing value of banded woodlands depends on the nutritive quality of the herbage layer as well as the palatability of the shrub and tree layers. In Australia, mulga (*A. aneura*) is regarded as an important source of browse for livestock, particularly during drought. However, mulga browse provides only a maintenance diet that requires additions of phosphorus and digestible energy either through supplementation or access to herbage (McMeniman and Little 1974; Pressland 1984).

Sheep production in mulga woodlands is limited by the availability of green herbage. More than 85% of the variation in live weight gain and wool production was accounted for by the mean annual availability of green herbage leaf. The avail-

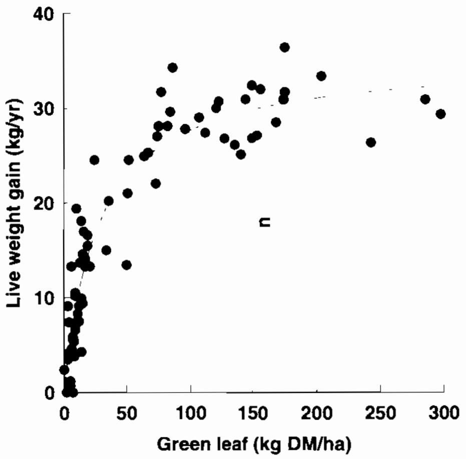

Figure 10.1. Relationship between the mean annual yield of green leaf from ephemeral and perennial herbage's and live weight gain in yearling sheep, r^2 = 0.87 (From Freudenberger, Wilson, and Palmer 1999.)

ability of dry herbage explained little variation (Freudenberger, Wilson, and Palmer 1999). Small increases in green herbage can result in large increases in livestock productivity until there is sufficient green leaf to support maximum growth (Figure 10.1).

The grazing value of banded woodlands in the West African Sahel appears to be less than that typically found in *Acacia* woodlands in Australia. The herbaceous fodder has a relatively high nutritive value while growing during the wet season, but these ephemeral plants quickly dry out and lose nutritive value during the long dry season and provide less than the maintenance nutrient requirements of livestock (Guerin et al. 1991). By the end of the dry season, there is often no herbaceous feed left. The nutritive value of browse in some of these Sahelian banded woodlands is poor. In the banded vegetation of southern Niger, 80% of the browse is composed of species of Combretaceae (e.g., *Combretum micranthum, Guiera senegalensis*), with an average protein concentration that is low (113 g kg DM^{-1}), and they contain high levels of tannin and lignin that depress digestibility (Geerling and De Bie 1988; Kone, Guerin, and Richard 1988; Lefèvre 1990). However, the species of Combretaceae are grazed at the end of the dry season when new buds and fresh growth are the few sources of green feed. Other browse species have a higher nutritive value and greater palatability (e.g., *Boscia angustifolia, Cadaba farinosa, Pterocarpus erinaceus,* and *Acacia* spp.); however, they are relatively rare within the banded woodlands of southern Niger (Achard 1997). However, in Burkina Faso, Mali, and Senegal, legumes such as *Pterocarpus lucens* and *Dalbergia melanoxylon* are often the dominant species and provide greater nutritive value.

Other Uses

The banded woodlands of the Sahel are the main source of fuel wood for villages, towns, and capital cities. For example, about 1 million persons live within a 150-

km radius of Niamey, Niger (50,000 km^2). Average fuelwood consumption is about 1 kg $person^{-1}$ d^{-1}, which represents 150,000 tonnes yr^{-1} just for the citizens of Niamey, most of it harvested from banded woodlands (Montagne and Mahamane 1996). In rural communities, less wood is cut, as villagers have access to millet stalks and manure. The estimated rate of production of marketable firewood (diameter, >4 cm) is 364,500 tonnes yr^{-1} within a 150-km radius of Niamey (Peltier, Lawali, and Montagne 1994). The firewood potential is large, but so is the demand from an ever-increasing urban and rural population.

Degradation of Primary Productivity

Banded patterning is not due to degradation. Banded patterning is reasonably resistant to breakdown, but when it occurs, loss of patterning may be irreversible in the short term (decades). The breakdown in patterning is characterized by the formation of erosion rills and gullies that run through bands of vegetation. Hiernaux and Gérard (1999) reported that bands have become fragmented near cattle tracks and particularly around villages with ever-increasing cultivation in the Sahel. Between 1950 and 1995, the area of banded vegetation decreased from 50% to 10% of total area, and bare runoff area increased from 50% to 90% of the total area at the Raneo site in Fakara region of southwestern Niger. Wickens and Collier (1971) described how runoff had intensified near a watering point in a landscape patterned with *Terminalia brownii* arcs in the Sudan. Runoff had become concentrated into rills that flowed through and around arcs. Insufficient moisture was flowing into the arcs, resulting in some areas of trees and shrubs dying from water stress. In banded regions of Somalia, Boaler and Hodge (1964) considered that arc patterns were resistant to breakdown except near permanent watering points where grazing is highly concentrated. Hiernaux and Gérard (1999) came to similar conclusions regarding the impact of grazing in west Africa.

In arid western Australia, Mabbutt and Fanning (1987) described how early stages of landscape deterioration first affected the contrast between runoff slopes and runon bands. Slopes lost their sparse cover of perennial grasses and shrubs; only ephemeral herbages persisted. Deterioration increased when runoff slopes and runon bands lost their continuity and failed to operate as closed systems; that is, water ran through or around bands. The late stage in vegetation degradation saw mulga bands reduced to series of aligned "islands" increasingly enveloped by bare surfaces. Mabbutt and Fanning (1987) deduced that this loss in landscapes patterning was due to a century of overgrazing and drought. This deduction is supported by Hodgkinson and Cook (1995), who experimentally demonstrated that drought combined with overgrazing leads to high mortality of perennial grasses in patterned mulga woodlands in eastern Australia. Loss of these grasses in runoff slopes and runon bands has been shown to increase runoff and sediment yield and reduce infiltration (Greene, Kinnell, and Wood 1994).

Overgrazing is probably the major cause of pattern breakdown in banded vegetation, but there are other causes. Cropping appears to have fragmented banding in regions of the Sahel (Hiernaux and Gérard 1999). So too has firewood and timber harvesting near urban centers. A reduction in fire frequency appears to have also changed vegetation patterning in Australia (Noble and Tongway 1986). The prolonged absence of fire is thought to have allowed the proliferation of fire-sensitive shrubs at the expense of grasses resulting in a less patchy landscape, often devoid of a surface herbage layer resulting in less efficient capture of runoff and water-borne nutrients (Freudenberger, Hodgkinson, and Noble 1997).

Implications for Management

Banded vegetation patterns are indicators of reasonably intact landscapes that function to conserve scarce resources of water- and surface-entrained soil nutrients. However, landscape patterning can be lost through overconsumption by grazing, clearing, or wood harvesting. The loss of patterning is a result of loss of critical landscape processes. Banded vegetation patterns fragment and shrink when the surface flow of water becomes concentrated and runs through or around bands and patches. Bands shrink and fragment because the local supply of soil water and nutrients has declined.

Banded patterns are resistant to breakdown—they have persisted during centuries of human occupation and use. However, overconsumption by clearing and timber harvesting or indirect overconsumption by livestock does cause patterned landscapes to breakdown.

Summary

Herbage production is focused on the upslope edge of bands with trees and shrubs dominating the core and downslope edge of bands. In Australia, a few, primarily ephemeral species are found on runoff slopes whereas perennial grasses requiring greater and more prolonged periods of adequate soil water are found on the upslope edge and core of bands. In the Sahel of Africa, there is generally a greater concentration of production within bands, with little plant growth between bands compared with Australian banded landscapes. The area of runoff increases with increasing aridity.

Not only is plant production in these landscapes highly variable in space, it is also highly variable through time. This is a result of both variable rainfall as well as the spatial concentration of soil water by locally captured runoff. A rainfall event with little runoff may induce a small pulse of growth, but a locally large pulse may be supported if the same rainfall event results in runoff into runon patches of vegetation.

Banded vegetation has been used for centuries or longer and have generally persisted, although are highly dynamic. In both Australia and Sahelian Africa, banded woodlands are important for grazing of livestock, with the additional demand for firewood in the Sahel. However, overconsumption by people and by their livestock can lead to the breakdown of landscape patterning. This occurs when runoff runs through or around patches because too much soil cover has been consumed. Without adequate cover, runoff is inefficiently captured within bands, and runoff "leaks" out of these two-phase mosaics. Patches break down because of increased aridity caused by poor capture of run off.

The causes of human-induced overconsumption are numerous and complex but need to be understood to avoid further loss of landscape patterning and to institute restoration procedures, which is the subject of Noble and associates (chapter 11, this volume).

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11. Toward Improved Management of Arid and Semiarid Banded Landscapes

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Introduction

Regularly patterned vegetation in arid ecosystems has been well documented in diverse regions of the world including northern Mexico (Montaña 1992), Sudan (Wickens and Collier 1971), South Africa (van der Meulen and Morris 1979), and Jordan (White 1969). Such patterning has been attributed primarily to endogenous landscape processes, particularly those relating to redistribution of rainfall (Boaler and Hodge 1962; White 1971; Cornet, Delhoume, and Montaña 1988; Greene 1992; Stafford Smith and Pickup 1993; Ludwig, Tongway and Marsden 1994; Ludwig and Tongway 1995; Thiéry, d'Herbès, and Valentin 1995; Tongway and Ludwig 1995; Dunkerley 1997).

In this chapter, we discuss the management of banded woodland vegetation in arid and semiarid landscapes of both Australia and the French-speaking countries of West Africa. In Australia, groved *Acacia aneura* (mulga) communities (Mabbutt and Fanning 1987; Tongway and Ludwig 1990) are clearly visible, especially from the air (Figure 11.1a). Similarly, in West Africa extensive areas of both tiger bush (*brousse tigrée*) (Figure 11.1b) and spotted bush (*brousses tachetées*) have been widely reported (Clos-Arceduc 1956; White 1970; Serpantié, Tezenas du Montcel, and Valentin 1991; Thiéry, d'Herbès, and Valentin 1995; Seghieri et al. 1997).

In particular, we focus on the central role of landscape function in determining future management approaches. Function in this context is defined as the collective landscape response to changes in rates of ecological processes mediating the

a

b

Figure 11.1. (a) Aerial view of mulga (*Acacia aneura*) grove/intergrove banding in central Australia looking south toward the Blackstone Range. (Photo: I.R. McLeod.) (b) Ground view of banded mulga in western New South Wales looking downslope. (Photo: J.C. Noble.)

distribution of soil water and nutrients, which, in turn, influence the local patterns of primary and secondary productivity (Tongway and Ludwig 1990). Any interference with this fundamental process may have significant repercussions on vegetation dynamics (Seghieri and Galle 1999), particularly those relating to herbage productivity (Noble, Greene, and Müller 1998) (Figure 11.2). In the case of banded landscapes, the maintenance of the banded structure is the first general rule that must be established across the whole spectrum of the society using these landscapes.

An ability to predict change in arid and semiarid landscapes following any specific management intervention requires an adequate understanding of the attributes and processes organizing the ecosystem under consideration (Cattelino et al. 1979; Noble and Slatyer 1980; Brown 1994). To be effective, however, as well as being acceptable to those currently using and managing the land, any particular management option must be seen as only part of a total management package integrating socioeconomic, natural resource, and animal husbandry components (Noble and Brown 1997; Noble, MacLeod, and Griffin 1997).

Holling (1992) defined three broad ranges of ecosystem scale (macro-, meso-, and microscale), each characterized by different dominant processes (Table 11.1). Vegetative processes dominate the microscales, whereas at the other extreme, geomorphologic and evolutionary processes are most influential at the macroscale level. The intermediate mesoscales, however, are dominated essentially by the ef-

Figure 11.2. Dry matter production by *Thyridolepis mitchelliana* (bandicoot or mulga mitchell grass) growing in an interception zone has been severely inhibited by metal barriers preventing entry by redistributed rainwater. Lake Mere Station, Louth, New South Wales.

Table 11.1. Hierarchical Scales in a Semiarid Savanna Landscape[a]

Scale	Space (km)	Time (yr)	Structural components	Structural processes
Micro	0.0001–0.001	0.1–2	Individual organisms (e.g., age, condition)	Physiological (e.g., photosynthesis)
	0.001–0.01	1–10	Population of individuals (e.g., species density, size)	Phenological (e.g., flowering)
Meso	0.01–0.05	10–100	Patches of individuals (e.g., clumps of vegetation)	Autecological (e.g., dynamics)
	0.05–1.0	10–100	Communities of populations (e.g., species composition)	Synecological (e.g., competition)
Macro	1.0–100	100–1000	Landscapes of communities (e.g., local patchiness)	Geomorphological (e.g., landforms)
	100–>3000	1000–10,000	Biomes—regional landscapes (e.g., life-forms, climates)	Tectonical (e.g., uplifts)

[a] From Holling (1992).

fects of animals, fire, water, wind, and especially people and are therefore most amenable to management.

It has been postulated (Tongway and Ludwig 1994) that robust or resilient landscapes tend to be dominated more by lower mesoscale (50 to 200 m) topographic regulatory mechanisms, such as slope/flat formations. However, fragile landscapes are more prone to catastrophic landscape dysfunction because they are regulated more by more temporary plant/soil mechanisms operating at low microscales (1 to 10 m). Rehabilitation of dysfunctional landscapes must therefore concentrate principally on restoring resource control mechanisms at whatever scale is deemed appropriate. In the case of less resilient ecosystems, this may best be achieved by reconstituting microscale processes on the scale of log hummocks (i.e., 0.5 to 5 m) (Noble, Diggle, and Whitford 1989; Tongway, Ludwig, and Whitford 1989). At this scale, soil processes such as water infiltration and organic matter cycling are basically mediated by soil invertebrates (Greene 1992). However, most management decisions in Australian rangelands are made at the individual field or paddock level involving communities of plants at scales ranging from 50 m up to 1 km (Noble and Brown 1997). The effect of mesoscale activities involving either grazing or fuel gathering ultimately depends on the cumulative effects of finer microscale processes inextricably linked to the growth of individual plants, whether woody or herbaceous.

Clearly, any form of land use that interferes significantly with such fundamental landscape processes as rainwater redistribution or nutrient cycling patterns will, in turn, have a negative effect on the vegetation's primary productivity potential. It is appropriate, therefore, to examine the respective impacts on landscape function of current land-use systems in both Australia and Niger. In this chapter, we describe the various land uses used in banded vegetation of both countries and their impacts on landscape function. We will also discuss principles to be applied when developing future management strategies aimed at conserving, and rehabilitating mesoscale landscape processes and thus achieve the sustainable use of these distinctive landscapes.

Comparative Land-Use Systems and Impacts on Landscape Function

Australia

The imposition of sedentary pastoralism by European settlers occurred rapidly throughout much of semiarid Australia during the second half of the 19th century following the advent of fencing wire in the 1860s (Pickard 1992). Before this, the country had been populated by a relatively small number of hunter-gatherer Aborigines (Tindale 1974) whose activities were regulated primarily by seasonal conditions although they were capable of surviving extremely arid conditions (Noble and Kimber 1997). Furthermore, the principal native herbivores, mainly *Macropus* spp. (kangaroos), were highly mobile and low in number and moved in response to seasonal conditions and the availability of ephemeral forage growing after scattered showers (Newsome 1975). The grazing pressure on the basic resources of soil and vegetation was thus controlled essentially by climate, forage, and surface water availability.

Although European-style pastoralism relied initially on natural waters, the discovery and use of artesian water from 1879 onward (Noble et al. 1998), especially in the mulga lands, and the construction of earthen tanks enabled domestic livestock to survive long into droughts. This ultimately led to pressures being placed on the soil and vegetation resources to which they were previously unaccustomed. Construction of permanent watering points quickly led to the development of a clearly visible grazing gradient with heavy grazing close to the water basically removing all accessible forage (Figure 11.3). Environmental problems generated by increasing numbers of domestic (sheep and cattle), feral (goats and rabbits), and native (kangaroos) herbivores were further accentuated by severe drought conditions experienced at the turn of the century (Noble and Tongway 1986a).

Mulga (*Acacia aneura*), the principal woody species in Australian banded landscapes, is commonly regarded as a seasonally important source of "topfeed" for livestock during extended droughts (Moore 1972). Large areas of *A. aneura* were either cut down by hand or pushed over mechanically during drought, although serious concerns have since been expressed about the ability of these plant communities to regenerate in some areas following such drought exploitation. Although remnant groves of *A. aneura* still appear to have superior herbage production

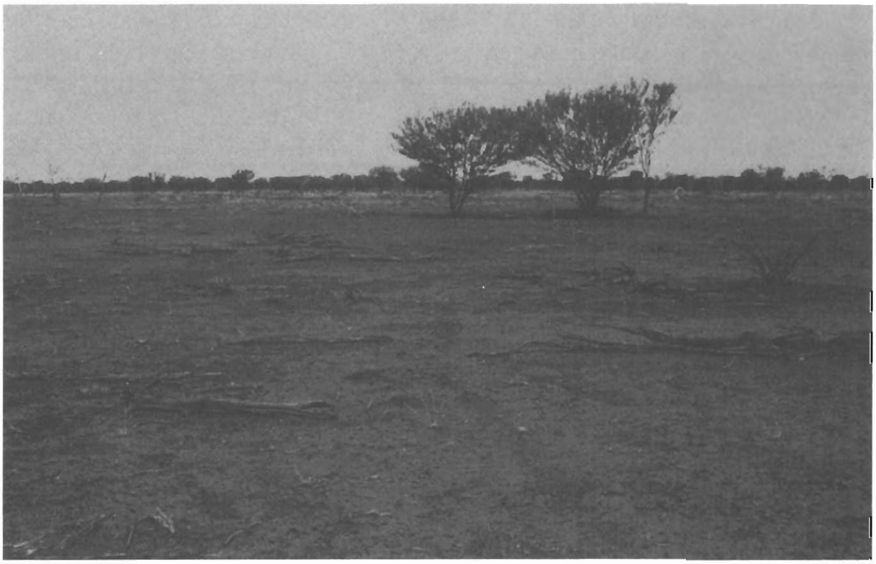


Figure 11.3. View of a remnant *Acacia aneura* (mulga) grove at Lake Mere station, New South Wales. Heavy prolonged grazing pressure has permitted erosion to remove fertile grove soil and destroyed the grove's capacity to trap water, topsoil, and litter. Perennial grasses have disappeared, and mulga trees are dying.

potential compared with other zones, it is uncertain whether this potential has been degraded significantly over time following drought feeding of mulga (see Figure 11.3).

Niger

In Niger, although the banded Sahelian formations (comprising 1 million ha) are important for both grazing and family cropping purposes (e.g., gums, fruit, edible leaves, and small game), the woody overstory in these landscapes is also intensively utilized as a source of domestic energy (Peltier, Lawali, and Montagne 1994). Although theoretically protected by law, in practice it has been virtually impossible for governments to impose any controls and herdsmen, professional woodcutters and local wood gatherers have had virtually unimpeded access to these resources. Under Nigerien forestry law, only harvesting of dead wood has been authorized, but local villagers admit to regularly harvesting some live wood as well. Trees of the Combretaceae including *Combretum micranthum, C. nigricans,* and *C. glutinosum,* together with *Cassia sieberiana, Acacia ataxacantha, A. macrostachya,* and *Sclerocarya birrea,* have all been harvested in the tiger bush "thicket zone" (Peltier, Lawali, and Montagne 1994; Thiéry, d'Herbès, and Valentin 1995). For commercial reasons and to reduce the risk of being apprehended if larger, more valuable trees are felled, woodcutters have relied on a coppice-based system or "furetage" whereby only the largest stems are cut from multistemmed coppices regenerating from base of cut trees. The original trunks are used to provide building timber, and the top residues are used as fuel.

Fuel consumption studies undertaken as part of the "Energie II" project funded by the Danish government through the World Bank have found that 95% of the domestic energy requirements of Niamey can be met by local wood supply (150,000 tonnes in 1994). Fuel is derived principally from the lateritic plateaus where tiger bush predominates (Matly 1990; Bertrand 1991). Total consumption was estimated to represent an annual harvesting of 50,000 to 80,000 ha of tiger bush, which, in reality, was dispersed over a much larger area averaging only a few stere (i.e., cubic meters) per hectare. Timber production from native forests in the Niamey region where rainfall ranges from 200 mm in the north to 500 mm in the south has been estimated at 1 million stere yr^{-1}, half of this being used by the city (Peltier, Lawali, and Montagne 1994).

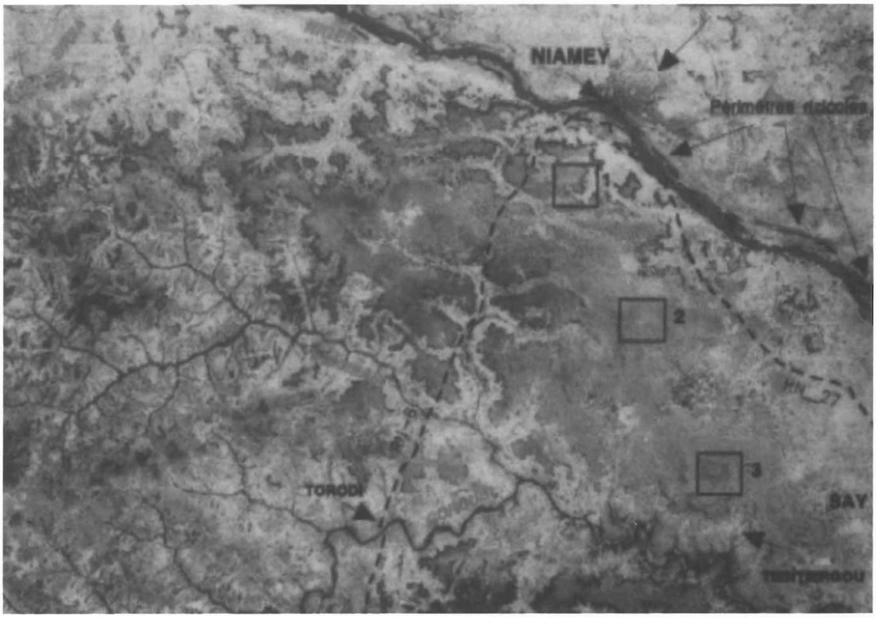
With a population of about 1 million persons, demand for fuel by Niamey's inhabitants is most intense in the immediate environs with a decreasing gradient of exploitation, clearly visible on satellite imagery (Landsat TM 185 × 185 km), as distance increases from the city (Figure 11.4). This periurban region represents a zone of intense resource exploitation. The intensity of fuel extraction can be gauged from the results of surveys indicating that average consumption of firewood in Niger is close to 1 kg $inhabitant^{-1}$ d^{-1}. By 1994, 150,000 tonnes of fuel were being harvested just for the citizens of Niamey alone, and zones of desertification had clearly evolved within a 20-km radius of the city (Montagne and Mahamane 1996).

Cattle are permitted to graze banded landscapes during the wet season, as palatable herbaceous species such as *Microchloa indica* and *Cyanotis lanata* and drinking water are both available. In the dry season, the cattle are removed from the banded plateau and allowed to graze on crop stubble in the lowlands. Herbage in the banded landscape has low digestibility in the dry season. There is no evidence at the Banizoumbou site in Niger that these herbage species regulate resources flowing into the grove (Seghieri and Galle 1999), although anecdotal evidence from Burkina Faso suggests that tall perennial grasses there may act as sinks for resources (P. Hiernaux, pers. comm.).

Recent studies in *Acacia aneura* banded landscapes in western New South Wales, however, has indicated that light-to-moderate grazing pressures were important in maintaining efficient landscape function thereby enhancing herbage production in the interception zone (Noble, Greene, and Müller 1998). Concurrent herbage production measurements in nonpatterned landscapes in the same region provided evidence supporting Noy-Meir's (1985) hypothesis that herbage production after a given rainfall event is higher in those landscapes where topographic source and sink zones exist.

During the severe droughts of the 1980s in Niger, a considerable proportion of drought-sensitive species in tiger bush country succumbed. Consequently, many cattle herds left the north Sahelian zone to take refuge in the south Sahelian or Sudanien regions. Here, they imposed heavy grazing pressures that eventually led to

a



b

Figure 11.4. (a) Satellite image illustrating the firewood harvesting gradient surrounding the city of Niamey; the light areas (1) near the city reflect intensive periurban wood harvesting, whereas the darker zones (2) and (3) farther away exhibit increasingly dense vegetation. (b) Authorized firewood logging can still lead to excessive exploitation. (From Peltier, Lawali, and Montagne 1994.)

a marked decline in the regeneration capacity of the grasslands because they were unable to seed down (Peltier, Lawali, and Montagne 1994). With less vegetative cover, normal rainfall now causes excessive runoff. In theory, these banded landscapes have a low cattle carrying capacity (0.1 head ha^{-1} yr^{-1}) and are generally only used by livestock during certain periods of the year. Because cattle are subject to transhumance (i.e., seasonal movement of livestock from one region to another) and graze primarily on crop residues, it is reckoned instead that 1 ha of mixed bush, in fact, provides the annual fodder requirement for one head of cattle (R. Peltier, unpublished data).

The potential for woody browse species in mixed bush to provide valuable fodder at key times has been reviewed elsewhere (Piot et al. 1980). More recently, Hiernaux and Gérard (1999) suggested that selective cutting might favor growth by suitable browse species such as *Pterocarpus lucens* and *Ziziphus mauritiana*.

Excessive harvesting of timber resources further exacerbates ecological degradation through accelerated erosion and subsequent loss of topsoil and nutrients. Future management is therefore aimed at ensuring that the ratio of vegetated surface to total plateau area returns as quickly as possible to the level required to sustain land resources under current rainfall regimes. Management strategies therefore need to be developed jointly with villagers to ensure that the interests of loggers, gatherers, and cattle breeders are all reconciled while maintaining basic ecological functioning of tiger bush ecosystems.

Toward Sustainable Land-Use Systems in Banded Landscapes

Future sustainable management of banded landscapes should be aimed at retaining and, when necessary, restoring optimum landscape function. Not only do management goals and objectives need to be clearly identified and articulated but their future refinement is dependent on the capacity to objectively monitor the effects of past decisions (Scifres and Hamilton 1993).

Decisions surrounding the management of natural resources often affect the scope for and outcomes of subsequent management actions for periods extending to decades (Scifres 1987). In stark contrast, the feedback to management actions for agricultural systems in high-rainfall zones may be as short as a single growing season. A natural consequence of feedback from management actions and the predisposition of action to restrain or enhance the scope for future action is to create a decision environment requiring a dynamic and iterative approach to management. This is particularly true of decisions relating to the selection of technologies and practices aimed at the rehabilitation of landscape function.

Strategies to manage landscape processes in a patterned landscape therefore need to be viewed as an integral component of the total management package required to retain solvency, if not growth, of business enterprises. That is, decision making to retain or enhance landscape function needs to be consistent with the principles of whole-enterprise management planning, whether it be a pastoral property in the mulga region of Australia or a village cooperative in Niger. In Niger, however, problems have arisen because fuelwood is considered a commodity to be freely harvested and sold. Price is largely dictated by labor costs involved in harvesting and transportation, as well as supply and demand. Because of this culture of unregulated exploitation, rural populations are not encouraged to manage the resource in a sustainable manner so that accelerated resource depletion has, in turn, led to subsequent landscape dysfunction. There are complex, long-standing sociopolitical structures that will exert an inertial effect on the uptake of new management options.

The sustainability of Niger's natural banded woodlands is threatened by a combination of several factors including climate (drought), humans (a consequence of increasing population, cultural traditions, and archaic production techniques), and livestock (excessive grazing pressures). Sustainable use of Australia's banded mulga is similarly constrained by multiple interdependent factors. These include extended drought allied with excessive grazing pressures imposed by an array of animals including domestic (sheep and cattle), feral (goats and rabbits), and native (grey and red kangaroos) herbivores and market forces in relation to the value of the products and their cost of production. Human factors differ, though, and relate more to declining commodity prices (e.g., wool), minimal potential for enterprise diversification, and marginal property size.

A problem-solving approach that simply looks at single factors or processes in isolation will only have a limited impact on future resource management in both countries. Although this approach may have been successful in reducing variability of the ecological target, there have usually been slow synchronous changes in the ecosystem. Spatial homogenizing of ecosystems has often led to situations in which systems change into persistent degraded states. Mechanical clearing of *Acacia cambagei* (gidgee) woodland in western Queensland, for example, has resulted in subordinate shrubs such as *Eremophila mitchellii* (budda), *E. gilesii* (green turkey-bush), and *Myoporum deserti* (ellangowan poison bush) becoming dominant to the exclusion of useful herbage species (Noble 1997).

Such negative sequences following inappropriate management intervention are only broken when the issue is seen as a strategic one of adaptive management, of science at the appropriate scales, and of understanding system behavior, not one of merely developing better technology (Holling 1978, 1995; Walters and Holling 1990). This requires

- flexible, adaptive, and integrated strategies, not rigid locked-in ones
- management and planning for learning, not simply for economic or social product
- monitoring designed as a part of active interventions to achieve understanding and to identify remedial response, not monitoring for monitoring's sake
- alternative scientific approaches, not just rigorously controlled experimental science

Adaptive management implies a systems-based approach to examining various ways in which natural systems (in this case, banded ecosystems) interact with human systems (social, economic, and political). It hinges on being able to measure the outcome of particular management strategies and to quickly and efficiently adapt them when necessary by using community dialogue to facilitate development of, for example, computer-based decision support systems. There is now a growing recognition that research also has to become an integral part of any resource management system. For active adaptive management to be effective, it is essential that landholders, in addition to other relevant stakeholders, participate in this collaborative process right from the beginning so that improved management strategies are rapidly applied.

To address the problem of developing rational management policies for the natural woodlands in Niger, the Household Energy Strategy (HES) was created in 1989 to encourage fundamental modifications of formerly exploitative harvesting methods. The strategy included but was not exclusive to banded woodlands. The strategy aimed at guaranteeing long-term production of wood for urban populations while creating income for those involved in fuelwood-related activities (Peltier, Lawali, and Montagne 1994; Montagne, Housseini, and Sanda 1997). The four main objectives of the HES were

1. to set a market value of a tree
2. to meet the fuelwood needs of rural and urban populations and to make them responsible for their local woodland
3. to create jobs and new income
4. to make future woodland management sustainable

This approach is essentially based on establishing sound fiscal policies, forest control, and rural markets. The fiscal policies provide legal guidelines for those involved in the fuelwood trade including state authorities, members of the management structures of rural markets, and trade carriers. Nigerien law authorizes the creation of production and fuelwood structures levying transportation taxes at the time fuelwood is purchased. Part of the taxes collected (40 to 60%) is remitted for woodland development projects such as agroforestry interventions, seedling nurseries, firebreaks, and erosion protection works. A share of the village receipt must also be spent on similar projects ranging from 30 to 50%, depending on the harvesting method used.

Rural fuelwood markets have been established to serve as incentives to villagers to practice sustainable development of woodland resources. “Oriental-type markets” are encouraged where there is a limited area of exploitation with a fixed quota on wood. Alternatively, “controlled markets” are appropriate for areas where the land is parceled for rotational harvesting. It is in the long-term interests of villagers to conserve their environment by using market mechanisms to exercise permanent control over the future exploitation of their woodlands. By forming cooperative groups of village markets, favorable fuelwood prices can then be negotiated with traders.

Once contracts have been signed between the state and rural wood markets, only contracted communities will be allowed to harvest wood for fuel purposes. By making villagers more aware of the value of a tree, they, in turn, become more aware of the need to protect and nurture the woodlands by only undertaking sustainable harvesting of fuelwood. An annual quota on wood to be exploited by rural markets will be fixed by environmental authorities, representatives of the management structure, and rural communities. If woodcutters fail to follow recommendations to enable regeneration of woodland resources, then the quota will be reduced or, if necessary, refused, resulting in either temporary or permanent closure of the rural market.

Rehabilitating Landscape Function

Degradation here is usually deemed to have occurred when there has been a measurable decline in the condition of the land (Noble, Cunningham, and Mulham 1984). However, the problem with this definition is that there has been an insufficient knowledge framework on which to base an objective determination of the trend in condition. Wilson and MacLeod (1991) have adopted a pragmatic stance by recognizing overgrazing (degradation) as having occurred in rangelands when there has been a measurable decline in animal production. This trend was more readily determined because of the ready accessibility of data detailing livestock numbers, wool production, and so on, on most pastoral properties. This definition is limited to a pastoral use and, in terms of other potential land uses such as the conservation of biodiversity, may be difficult to translate.

Degradation of biological diversity is usually more difficult to determine. Although there is increasing awareness of the need to develop sustainable management practices in Niger, less emphasis appears to be directed toward nature conservation issues. In Australia, however, conservation of biodiversity, both on and off nature reserves, is becoming increasingly important as the need to address land degradation problems on a national scale becomes more widely recognized by the wider community. Biodiversity comprises multiple levels of diversity of biological organisms and their interactions (Noss 1990; West 1993). Any measurable decline in genetic, species community, or ecosystem levels of diversity can therefore be classed as degradation.

The need for rehabilitation has therefore been clouded in a lack of understanding for some time.

The use of "topfeed"—cutting of edible tree canopy—during drought is not as widely practiced now since excessive felling of *A. aneura* in the past has often led to major landscape degradation following accelerated erosion and declining regeneration of both *A. aneura* and perennial grasses (Noble and Tongway 1986b). However, in such cases, felled *A. aneura* trees should be aligned parallel with land contours so that the stems and branches effectively trap surface runoff, as well as any transported topsoil and organic material (Figure 11.5).

In experiments conducted in northwestern New South Wales, Ludwig and Tongway (1996) and Tongway and Ludwig (1996) demonstrated the effectiveness of such brush piles in creating fertile patches and ultimately rehabilitating degraded landscapes. After just 2 to 3 years, significant accretion of surface soil and litter was measured underneath felled *Acacia aneura* on Lake Mere station with upper

Figure 11.5. *Acacia aneura* (mulga) scrub pulled for drought feeding on Westmere Station, west of Bourke, New South Wales. The pulled trees have been aligned parallel with the contours to minimize erosion and to trap any topsoil, organic matter, and seeds transported by rainfall runoff. (Photo: J.C. Noble.)

surfaces 3mm higher than adjoining control sites. These "engineered" hummocks essentially behaved as "islands" of enhanced fertility. Not only did soil nitrogen and carbon increase by 30% in the soil hummock developing beneath the piles, but there was also a 10-fold increase in infiltration and a fourfold increase in the abundance of soil invertebrates (Tongway and Ludwig 1996). In addition, felled canopies effectively acted as grazing exclosures preventing defoliation by vertebrate herbivores thereby enabling desirable forage species, especially perennial grasses, to reestablish and set seed.

The general improvement in road transportation of livestock today enables pastoralists to move their livestock elsewhere where feed is available or, alternatively, sell them (Noble and Tongway 1986a) rather than risk degrading soil and vegetation resources by interfering with the established landscape processes. This is a "passive" method of rehabilitation, relying on lack of grazing pressure to allow grasses to recuperate or germinate after the break in the drought.

Past reclamation procedures in Niger initially have involved reforestation procedures using a wide range of exotic species (e.g., *Eucalyptus camaldulensis, Acacia holosericea, A. senegal,* and *A. nilotica*), none of which grew in banded formations in their countries of origin. Furthermore, seedlings were planted in an unnatural pattern (5 × 5-m grid) that failed to recognize the fundamental importance of restoring previous landscape processes (R. Peltier, unpublished data). Subsequently, by the early 1990s, state and financial backers had recognized the general ineffectiveness of these programs because of continuing felling and grazing combined with general 'dieback' in plantations. It was with this background that the Danish government ultimately decided to finance the "Energie II" project described earlier.

Limitations of single-option approaches to rangeland management have, in many cases, been accentuated by an inadequate understanding of landscape function. Although integrated pest management is now widely established in agricultural systems (Norton and Mumford 1984), fully integrated systems for managing landscape function in rangelands are yet to be developed. The rationale for integrating several different rehabilitation technologies within a single system is to capture the synergism of the suite of treatments that would not ordinarily manifest themselves if the treatments were applied in isolation or in a different ordering of application. In this context, properties emerging from integrated shrub management systems (Scifres 1980, 1986) may eventually result in significant improvement of landscape function.

Summary

The studies reported in other chapters in this book indicate that common ecological principles are at work across all the banded landscapes. However, it is hardly surprising that any comparison of arid land management policies in two countries such as Australia and Niger is heavily constrained by contrasting socioeconomic considerations. Stark contrasts in national wealth and standards of living experienced by people who live in either so-called developed or developing economies are clearly reflected in contrasting land management imperatives. Management of timber resources in Niger, for example, bears little resemblance to standard management procedures used by foresters in developed countries. Instead, Nigerien timber management aims to meet fuelwood demand in the most cost-efficient way possible by forcing communities to take responsibility for managing their own local woodlands. Nonetheless, management planning still remains an important element in the setting of harvesting quotas, boundaries between villages, and the parceling of land designated for exploitation.

In essence, contrasting emphases on resource use in banded communities in both countries represent extremes of a continuum. The most intense utilization of land resources occurs at the Nigerien end of the continuum where production of food, pharmaceuticals, and fuelwood are the major imperatives of what is primarily a subsistence economy. The opposite end of the spectrum representing less intense resource use is apparent in the more affluent economies found in countries such as Australia, where a production surplus of commodities such as meat or wool is usually available for export. Perceptions of the value of woody components of banded communities may also differ markedly. In Niger, basically all woody plants growing in *brousse tigrée* represent potential fuel. By contrast, the proliferation of shrubs and small trees ("woody weeds") throughout the semiarid woodlands of eastern Australia is perceived instead to be symptomatic of land degradation (Noble 1997).

Future management of banded landscapes is heavily dependent on monitoring systems designed to identify and quantify changes in productive potential. Monitoring procedures, based on the ecological principles articulated in this book, can be divided into two types. First, the newly emerging generation of rangeland process and decision support models such as SEESAW (Simulating the Ecology and Economics of Semiarid Woodlands) (Ludwig, Sinclair, and Noble 1992) and RANGEPACK (Stafford Smith and Foran 1990) offers considerable scope for a scientific level of ecosystem function assessment. Field procedures using simple indicators but also based on the ecological principle of landscape function are being used by Australian government agencies (Tongway 1994; Tongway and Hindley 1995). Over time, the application of monitoring information can then be refined through a process of active adaptive management (Walters and Holling 1990; Holling 1995).

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12. Banded Landscapes: Ecological Developments and Management Consequences

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Introduction

Most of the studies on banded landscapes have been carried out by groups totally isolated from each other, divided by language, culture, and differing objectives. This book has been structured into distinct themes ranging from the global distribution of these landscapes to their management strategies to synthesize this dispersed knowledge and facilitate the cross-linking of concepts and information. One of the aims of this volume was to integrate the scattered knowledge on banded landscape function to the level of ecological principles to be applied to more complex situations.

The literature on vegetation patterning is wealthier in hypotheses than in corroborating data. This concluding chapter discriminates and discusses the issues that have been clearly demonstrated and widely accepted from those that are still debatable or speculative. This leads us to identify the priorities for future research. We then examine the main lessons that can be learned from the banded vegetation pattern in the broader contexts of landscape ecology and land management. These conclusions are based on the various chapters of this book as well as from the recent special issues of *Acta Oecologica* (Tongway and Seghieri 1999) and *Catena* (Valentin and Poeson 1999) and from other recent publications.

Banded Landscapes: Established Principles of Structure and Function

The following discussion synthesizes the factors and processes now considered as intrinsic to all banded vegetation patterned landscapes.

Co-occurrence of Critical Factors in Banded Landscapes

With the exception of wave-regenerated forests and the ancient suppressed dunes (chapter 1, this volume), it is now well established that vegetation patterns occur only where particular critical combinations of soil properties, topographic shape, and rainfall characteristics are met. These factors must, in general, favor water runoff sufficient to produce sheet overland flow over a distance of few tens of metres but insufficient to trigger the concentration of runoff into rill-flow (chapter 4, this volume).

Soil Properties

There is now general consensus among researchers that differences observed in the soils of bands and conjugate interbands are a consequence of banding rather than a cause (Bromley et al. 1997). Banded vegetation develops on medium-textured soils with low infiltration capacity often due to surface crusting (chapter 4, this volume). Banded vegetation does not occur where sandy deposits locally cover impermeable soils (chapter 1, this volume). Existing banded vegetation collapsed in Mali when wind-borne sands were extensively deposited as a consequence of desertification (Chapter 6, this volume).

Topography

Banded vegetation occurs on planar surfaces with sufficient slope to enable sheet overland flow to initiate. In flat landscapes with a nondirectional runoff pattern, the vegetation is no longer banded but spotted (chapter 1, this volume). Banded vegetation occurs on slopes ranging from as low as 0.12% in Sudan (Worral 1960) to 40.4% in a Mediterranean regime (Cammeraat and Imeson 1999), even though the annual rainfall is similar (250 mm). Slope also controls the wavelength (band plus interband width) of the pattern even at local scale: the wavelength decreasing exponentially with increasing slope gradient (d'Herbès and Valentin 1997; Eddy et al. 1999).

Climatic Regime

Banded vegetation develops under arid and semi-arid conditions, with annual rainfall ranging from 75 mm yr^{-1} in Jordan (White 1969) to 640 mm yr^{-1} (Valentin and d'Herbès 1999). All banded landscapes are subject to a water shortage of some sort. Rainfall can vary from low and nonseasonal, as in Australia (Mabbutt and Fanning 1987), to moderate but highly seasonal, as in Niger (Galle, Ehrmann, and Peugeot 1999). In such a range of circumstances, banding can then be interpreted as a biotic evolutionary "strategy" for surviving lack of available soil water. The bands accumulate runoff water and the biological systems in them function as though they were in a higher rainfall climatic regime (Noy-Meir 1973).

Optimal rainfall for banded patterns has been derived from statistical and simulation studies for a range of different climatic regimes (Table 12.1). This optimal value increases with increasing percentage of high rainfall events and the mean monthly minimum air temperature and decreasing duration of the rainy season.

For a given slope gradient, the contrast between the band and interband becomes less distinct as mean annual rainfall increases (Valentin, d'Herbès, and Poesen 1999) and as the rainfall distribution becomes more even throughout the year (chapter 10, this volume). Further, in a given region, the mean annual rainfall controls the interband/band ratio (Valentin and d'Herbès 1999).

Although banded landscapes develop across a wide range of soil, topographic, and climatic conditions, the recent research has shown that they occur only where the co-occurrence of several critical conditions are met. This explains why such patterns do not occupy much larger proportions of arid and semiarid regions. The fact that most studies have been concentrated in Australia, Sahelian Africa, and Mexico (chapter 1, this volume) does not preclude the occurrence of banded patterns in other parts of the world (e.g., Asia).

Processes That Maintain Banded Patterns

Although the role of wind cannot be overlooked in certain circumstances (Leprun 1999; chapter 1, this volume), surface hydrological processes are critical to the ongoing functioning of banded landscapes. These lands are excellent natural laboratories, demonstrating the principles of water and nutrient conservation in space and time. Three main processes are involved: obstruction to overland flow, differential infiltration, and efficient nutrient cycling. Feedback loops stabilize the operation of this "resource control" system (chapter 2, this volume).

Overland Flow

The banded patterns act as a natural water harvesting system, the overland flow produced from the bare and impermeable interbands running onto the bands (Valentin and d'Herbès 1999; chapter 4, this volume). The runoff coefficients (volume of total runoff/volume of total rainfall, %) ranges in the interbands from 23% in southeastern Spain (Bergkamp, Cerdà, and Imeson 1999) to 75% in northern Mexico (Janeau, Mauchamp, and Tarin 1999). Vegetation bands tend to obstruct or regulate sheet-flow so that sediments and organic matter are continually being deposited and conserved within the bands, forming a natural bench structure that favors resource retention (Dunkerley and Brown 1999; Valentin, d'Herbès and Poesen 1999; chapter 2, this volume).

Table 12.1. Optimal Annual Rainfall as Influenced by Climatic Regime[a]

Optimal annual rainfall (mm)	Seasonal rainfall distribution	Rainfall events distribution	Mean monthly minimum air temperature (°C)	Site and authors
250	75% in 6 summer months	20% (>12.5 mm)	3.9°C—July	Central Australia Slatyer (1961)
280	70% in 4 summer months	20% (>10 mm)	3.9°C—January	Northern Mexico Delhoume (1996)
390	Autumn and spring	35% (>15 mm)	9.3°C—January	Southeast Spain Cammeraat and Imeson (1999) Bergkamp et al. (1999)
550	90% in 3 summer months	40% (>10 mm)	15.9°C—January	Southwest Niger Galle et al. (1999) Valentin and d'Herbès (1999)

[a] See also chapters 4 and 5 (this volume).

Differential Infiltration

Rainwater redistribution is caused by higher infiltration rates in the bands compared with the interbands (chapters 4 and 5, this volume). These differences are mainly controlled by the surface soil properties of the respective zones. Physical and biological crusts dominate the interpatch zones, resulting in low infiltration rates (Eldridge 1999; Janeau, Mauchamp, and Tarin 1999; Macdonald, Melville, and White 1999; Malam Issa et al. 1999; Valentin and d'Herbès 1999), whereas vegetation, litter, and bioturbation effects facilitate high infiltration rates in the patches (Greene 1992; Seghieri and Galle 1999; chapter 6, this volume).

Due to this rainwater redistribution, the bands receive from two (in southeastern Australia) (Tongway and Ludwig 1990) to four times (locally eight, in southwestern Niger), (Galle, Ehrmann, and Peugeot 1999) the rainfall at the site. The center of the bands has abundant biopores enabling effective water capture from the interband (Seghieri and Galle 1999). The upslope grassy band edge is intermediate (Greene 1992; Bromley et al. 1997).

Nutrient Cycling

In addition to substantial runon and high infiltration rates, the soils in the bands also concentrate more soil nutrients and organic matter than the adjacent interband soils (Guillaume et al. 1999; Tongway and Ludwig 1990; Ludwig, Wiens, and Tongway 2000; chapter 10, this volume). As a consequence, the vegetation bands are alternatively known as "resource islands" or "fertile patches" (Tongway 1990; chapter 6, this volume). However, the dynamics of nutrient cycling seem to have been little studied in either intact or degraded landscapes.

Maximizing Plant Productivity

Recent field data and simulations on banded landscapes have substantiated the theory of Noy-Meir (1973), which postulates that in environments with limited resources, plant productivity is higher if the resources are concentrated into patches instead of being uniformly dispersed over the landscape (chapter 2, this volume). In the Sahel, this resource concentration enables the formation of a forest system (Hiernaux and Gérard 1999; Seghieri and Galle 1999). The productivity of this discontinuous forest at least equals (Hiernaux and Gérard 1999) and can even double (Ichaou and d'Herbès 1997; Valentin and d'Herbès 1999) that of adjacent nonbanded landscapes. Similarly, a simulation model has showed that under southeastern Australian conditions, the productivity of a banded pattern landscape is more than twofold that of a landscape with no patchiness (Ludwig, Tongway, and Marsden 1999).

Although temporal variations in herbage yields were higher in banded systems than in nonbanded adjacent ones (Hiernaux and Gérard 1999), perennial plants commonly dominate the bands. This implies that sufficient water and nutrients are available to cope with either chronic or seasonal drought (see above).

Response of the Banded Landscapes to Climate Change

Most predictions concerning the possible response of banded landscapes to climate change have been derived from studies over the past 50 years (Hiernaux and Gérard 1999; chapter10, this volume) and from models (chapter 8, this volume). The systems can persist in the face of severe drought by adjusting the proportion of runoff and runon areas. A time response of 15 years illustrating this adjustment was monitored along a climate gradient transect about 200 km long, covering an annual rainfall range of 300 to 750 mm, by using air photos from 1950 to 1992 (Valentin and d'Herbès 1999). These results suggest that the runon zone cannot be maintained when the mean annual rainfall falls below 155 mm. Similar results (200 mm) were obtained from evapotranspiration assessments in the same region (Culf et al. 1993).

The scenario of expected climate change in eastern Australia (chapter 8, this volume), which includes warmer temperatures (+2°C), greater summer rainfall (+10%), and lower winter rainfall (–10%) indicates that the potential impact of changed land management (e.g., tree clearing or cropping) is far greater than any expected from climate change.

Response of Banded Patterns to Land Use

Banded patterning is sufficiently resilient to resist the stress and disturbance caused by traditional moderate land use. For example, Cammeraat and Imeson (1999) observed the resprouting of shrub bands after a forest fire in northeastern Spain. Major stress arising from overgrazing or excessive woodcutting and inappropriate land use (cropping) can lead to several stages of landscape degradation (chapter 10, this volume).

The earliest indicator of deterioration is the decline in the contrast between the two mosaic phases (Mabbutt and Fanning 1987). Overgrazing by domestic (sheep and cattle), feral (goats and rabbits), and native (kangaroos) herbivores is considered to be the prime cause of deterioration of banded landscapes in Australia (chapter 11, this volume). Persistent grazing with set stocking levels, coupled with drought, results in the death of perennial grass species (Hodgkinson 1993; Noble, Greene, and Müller 1998).

The occurrence of rills and gullies indicates the second stage of degradation in which water is lost rapidly out of the local ecosystem by concentrated rapid flows (Greene, Kinnell, and Wood 1994).

The late stage in vegetation degradation is characterized by disruption of the band pattern (Tongway and Ludwig 1997; Wu, Thurow, and Whisenant 2000). The bands may become shorter in length along the contour, narrower, or bisected by animal tracks. This pattern fragmentation results in a loss of landscape function and hampers rehabilitation. High stocking rates (0.7 to 0.8 sheep ha^{-1}) lead to such breakdown in landscape function and patterning (Tongway and Ludwig 1990; Wilson 1991) and in increased runoff and sediment yield (Greene, Kinnell, and Wood 1994; Tongway and Ludwig 1997; Ludwig, Tongway, and Marsden 1999; chapter 4, this volume). In Africa, vegetation bands become fragmented near cattle tracks particularly near villages and around watering points (Boaler and Hodge 1964; Hiernaux and Gérard 1999; chapter 10, this volume). Firewood and timber harvesting near urban centers and cropping are, however, more serious threats for tiger bush in West Africa (Torrekens, Brouwer, and Hiernaux 1997; Hiernaux and Gérard 1999; chapter 10, this volume). The clearing of tiger bush thickets to crop sorghum or millet, a marginal agricultural practice in itself, constitutes a "resource-mining" process that leads to desertified landscapes subject to severe wind and water erosion.

Unresolved Issues

Initiation of Bands

The preconditions for band initiation is a common thread through all the available literature but the least satisfactorily resolved. Models have demonstrated that banded vegetation patterns may result either from landscape degradation or rehabilitation (Thiéry, d'Herbès, and Valentin 1995; Dunkerley 1997), but the natural initiation of banded vegetation has never been observed (chapter 2, this volume). Many authors (Clos-Arceduc 1956; López-Portillo and Montaña 1999) consider that vegetation bands form from the coalescence of smaller patches, resulting for an increasing obstruction of sheet-flow and deposition of sediments (Bryan and Brun 1999; chapter 2, this volume) rather than from the degradation of a continuous vegetation cover (White 1971). However, this issue is likely to remain speculative in the absence of more abundant field evidence and long-term monitoring studies.

Upslope Movement of Vegetation Bands

The hypothesis that vegetation bands slowly migrate upslope is also a much debated topic. It is clearly intimately linked to the runoff/runon theory that underpins the basic functioning of banded vegetation. The obstruction of overland flow by the bands would favor the upslope germination of pioneer plants in this upslope edge and the decline of vegetation due to resource shortage at the downslope edge. Although the runoff/runon and/or source and sink theory has been clearly demonstrated by field measurements, the upslope movement of bands is still a matter of contention (López-Portillo and Montaña 1999; Valentin, d'Herbès, and Poesen 1999; Couteron et al. 2000; chapter 2, this volume).

An array of arguments has been proposed to support the upslope migration of bands based on the distinct zonal distribution of physical and biological components of the bands as well as direct and indirect assessments of vegetation dynamics. A sequence of soil crust types strongly supports the notion of soil deposition on the upslope edge of the bands (Valentin and Bresson 1992; Valentin and d'Herbès 1999). Marked gradients of soil organic carbon content provide corroboration (Tongway and Ludwig 1990; Guillaume 1999). Similarly, the presence of abandoned termite nests in the bare interband suggests the former presence of a vegetation band here (Ouédraogo and Lepage 1997; chapter 6, this volume). The strong similarity of subsoils between bands and interbands as observed by Bromley and colleagues (1997) supports the notion that subsoil properties do not preclude migration. This is not uniformly so. Banded mulga in Western Australia is underlain by a siliceous hardpan that is much deeper within the tree band than the interband (Mabbutt and Fanning 1987).

Seedlings are frequently observed to be concentrated on the upslope edge of the band (Montaña, López-Portillo, and Mauchamp 1990; Tongway and Ludwig 1990; Seghieri, Floret, and Ponanier 1994; Seghieri et al. 1996) Thiéry and associates (1995) called this zone the "pioneer zone." In addition, dead trees or shrubs are commonly reported near the downslope edge, suggesting that these plants had died as a consequence of resource "starvation."

The migration "velocity" of bands has been assessed on a subset of sites, by using a variety of methods including field monitoring with benchmarks, digitized aerial photographs, age distribution of trees with dendrochronology, and residual ^{137}C distribution in the soil, under a wide range of climatic and topographic conditions (Table 12.2). The fastest observed migration was 1.5 m yr^{-1} for grass bands, 0.8 for shrubs, and 0.8 for trees. At the global scale, the mean annual rainfall does not seem to influence migration velocity, neither does wind action despite its importance in Mali. However, at the local scale, faster migrations have been monitored in Mexico and in Niger during wetter years, the upward shift being less and even possibly nil during drier years (Montaña 1992). Although mulga bands may migrate upslope (chapter 2, this volume), it has not been reported in Australia.

Where migration has been detected and measured, most authors considered that it is highly variable in space and time. During dry years, the thicket vegetation density thins (Valentin and d'Herbès 1999; Couteron et al. 2000) and the downslope edge contracts due to plant death (Ambouta 1984; Wu, Thurow, and Whisenant 2000). Conversely, during the wetter years, the bands extend on the upslope edge, implying a net upslope migration (Ambouta 1984). Clearly, these processes are asynchronous.

The process of band movement at fine scale has been associated with differences in local slope at the upslope edge of the band that might influence the differential availability of water and seeds (Seghieri, Floret, and Ponanier 1994). The upslope edge of the vegetation band is often scalloped or wavy, with "prominences" and "bays" causing the capture of water, alluvium, and seeds to be uneven. Due to a very slight counterslope, the upslope migration might be less rapid in the prominences than in the bays. Over time, these microtopographic units would be expected to alternate.

Stationarity of some systems studied was attributed to the difference in the soil depth between bands and interbands as in Western Australia (Mabbut and Fanning 1987) or because of the even distribution of the age structure of shrubs across the bands in northern Mexico (López-Portillo and Montaña 1999).

At present, the evidence is that the upslope migration of vegetation bands is not an invariable property of the banded systems at the time scale of the observers. The question remaining unresolved is "What are the factors and processes controlling

Table 12.2. Velocity of Upslope Migration of Vegetation Bands

Country	Site	Mean annual rainfall (mm)	Mean slope gradient (%)	Mean annual velocity (m yr^{-1})	Method	Source
Mexico	Mapimi	184	0.37	0	Field monitoring of a peak of species richness (5 years)	Montaña 1992
Mali	Gossi	200	2.1	0.20	Field benchmarks (4 years)	Leprun 1992
Somalia	Northern region	213	0.22	0.15–0.30	?	Boaler and Hodge 1964
Sudan	Butana	250	0.36	0.3–1.5	Field benchmarks	Worral 1959
Mexico	Mapimi	311	0.37	0.80	Field monitoring of a peak of species richness (5 years)	Montaña 1992
Mali	N'Daki	300	1.9	0.25	Field benchmarks (21 years)	Leprun 1992
Mali	Hombori	450	0.9	0.75	Field benchmarks (21 years)	Leprun 1992
Niger	Sofiabangou	476	0.41	0.5	Dendrochronology (45 years)	D'Herbès et al. 1997
Niger	Hamdallaye	480	NA	0–0.65	Aerial photographs (1960–1992)	Wu et al. in press
Niger	Banizoumbou	495	0.27	0.19–27	^{137}Cs techniques (32 years)	Chappel et al. 1999
Niger	Banizoumbou	495	0.27	0.37–0.42	Extension of sediment crusts & dendrochonology (19 years)	Chappel et al. 1999

NA, not available

the upslope migration?" Permeable soils in the bare zone with low water runoff characteristics have been credited with the stability of the bands in northern Burkina Faso as compared with the migrating bands of Niger (Couteron et al. 2000). Different dynamics have been observed on sites located close by, leading to the interim conclusion that stationarity or movement of bands is a subtle dynamic involving climatic, geomorphic, biotic, and management interactions (López-Portillo and Montaña 1999).

The lack of a genuinely consistent theory here, linking different sites probably reflects complex issues that have not been adequately integrated at the conceptual level. Temporal scale is a major issue that may not be amenable to conventional studies over time scales typical of scientific experiments. Landscapes may well be operating at vast time scales or reacting to rare stochastic events such as drought, flood, and fire, or expanding and contracting according to seasonal variations. In this respect, grasses are likely to react more quickly to events than trees. It is an important process to fully understand, but comprehensive explanations are still in the future.

Priorities for Future Research

At the Global Scale

All the global occurrences of banded vegetation have not been yet identified. Observation of the macropattern in satellite images would enable this task to be effected with existing data. When located, the ecological principles presented in this volume should assist in dealing with the management issues of those lands. In particular, the well-understood outcomes of research to date at the ecological principal level should be deployed to avoid a new round of research ab initio.

At the Regional and Landscape Scales

Long-term monitoring needs to use extensive, remotely sensed data that should be calibrated against and integrated with ground-based measurements, so that the interpretation is based on processes and directed to management solutions (Wu, Thurow, and Whisenant 2000). Hyperspectral sensors will give more targeted information. These techniques will play a major role in extending the ecological principles understood at fine scale to the management and regional scale.

Manipulative experiments (Noble, Greene, and Müller 1998; Seghieri and Galle 1999; chapter 7, this volume) need to be directly related to rehabilitation or sustainable use rather than driven by just scientific curiosity. The human dimension should be thus more prominent, especially in long-term management experiments (chapter 9, this volume).

At the Local and Detailed Scales

We can distinguish three main themes: physical, biophysical, and purely biological processes. Although these have been separated for discussion, the integration of information from these areas needs to occur to provide insights into overall landscape functioning.

Physical

Processes under this heading comprise the interaction of climatic events with the soil/terrain system. Whereas the role of runon and runoff processes in regard to differential soil water storage have been clearly shown to be pivotal for banded vegetation, the effect of erosion and deposition processes have not yet been clearly elucidated. Water erosion and sedimentation are likely to greatly affect slope profile evolution (Bryan and Brun 1999; Valentin and d'Herbès 1999) and thus upslope migration. This migration should be studied further, by using such isotopic measurements as residual ^{137}Cs (Chappel et al. 1999). Further work is also needed on the origin and the role of wind-borne soil material, its accumulation in the vegetation bands, and its impact on texture, mineralogy, and fertility (Tongway and Ludwig 1996).

Biophysical

Soil biota and soil physical properties are intimately linked through bioturbation and soil organic matter decomposition dynamics. The impact of soil fauna on infiltration, as well as the structural stabilization of soil aggregates by soil organic matter, has been well established, but the reciprocal role of soil physics on the fate of soil organic constituent has still to be explored. For example, the natural abundance of ^{13}C in the organic matter associated with mineral soil particle fractions in Niger shows that although carbon from C_3 plants is the dominant contribution, carbon from C_4 plants was disproportionately high (Guillaume 1999). This raises questions about the differential carbon mineralization rates as between C_3 and C_4 plants and the role this might play in providing evidence about band movement. Such work needs to be substantiated under other circumstances, and the general principles will be relevant also to nonbanded landscapes in these climatic zones.

Biological

The use of vital attributes sensu Noble and Slatyer (1980) would be useful to identify the common and divergent properties of plants composing banded vegetation. Vital attributes are those of a species that are essential to its function in the vegetation intergenerational replacement and thus band maintenance. They include mainly, but not only, the arrival pathway and persistence at the site and the ability to establish and grow to maturity in the community. The assessment of plant functional attributes sensu Gillison and Carpenter (1997) and Walker, Kinzig, and Langridge (1999) would favor rapid and uniform assessment of plant properties as a response to variation in the physical environment at differing spatial scales, independent of species per se. Properties such as life cycle, physiological, and phenological features have been identified in Niger (Seghieri and Galle 1999). Structural-functional plant classification (also called "functional grouping") groups species with similar functional and morphological attributes such as root distribution and leaf area index, properties that are crucial to understand both resource utilization and the processes by which plants maintain themselves in the landscape (Box 1996). A comparison of the occurrence and distribution of functional groups between the different zones in a banded landscape would help to identify a framework of the common biological processes such as facilitation, tolerance, and competition/inhibition, as has been done for the physical processes.

Consequences for Landscape Ecology

The use of the neat geometrical arrangement of tiger bush has been used as a springboard to deal with ecosystems with more subtle spatial arrangements. Tiger bush lends itself well to modeling exercises (chapters 5 and 6, this volume) that are readily verifiable because the output is a distinctive pattern. The underlying process were generalized to apply to less overtly patterned landscapes to understand both their spatial arrangement and functioning (Ludwig and Tongway 1995). In the absence of a regular pattern as a starting point, this might have not eventuated. In turn, this has lead to a generalized framework by which to understand overall landscape function (Ludwig and Tongway 1997; chapter 2, this volume) and a monitoring system now implemented in Australia based on these principles (Tongway 1994; Tongway and Hindley 1995, 2000).

Consequences for the Management of Arid and Semiarid Environment

The lessons drawn from these banded patterns have lead to the recognition of heterogeneous landscape systems as being ecologically "sensible" and sustainable compared with homogeneous systems. In this respect, many traditional cultures in Africa have used resource-regulating structures in their cropping activities for centuries. Sometimes, modern methods based on European farming models have ridden roughshod over satisfactory traditional methods. For instance, water harvesting and runoff farming are simple to implement and more easily adopted by populations than irrigation in the Sahelian zone (Rockström and de Rouw 1997).

Rehabilitation of desertified banded landscapes will never be successful if complete vegetation of the previous band and interband zones is attempted (Thiéry et al. 1997). It is more sensible to create structures that favor trapping of runoff and sediments along the contour to rebuild vegetation patches. For instance, in a rehabilitation experiment, after 11 years the infiltration rate is about 320 mm hr^{-1}, compared with about 12 mm hr^{-1} for controls, which remain crusted interband zones (Tongway and Ludwig 1996; Tongway, Ludwig, and Hindley, pers. comm.).

Summary

The study of banded landscapes over the past 40 years has established a sound scientific basis for the understanding and management of banded landscapes. Some issues such as the initiation of the banding vegetation patterns remain unclear. What remains ahead is the development of the scientific principles that will underlie the sustainable use of banded landscapes in a range of socioeconomic settings around the world. Banded landscapes are likely to produce further sound lessons not only for the arid and semiarid environments but more broadly to landscape ecology and land management. Management guidelines will be improved over time as new information comes forward.

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